

PROCEEDINGS OF THE LINNEAN SOCIETY OF LONDON

153rd Session (1940-41)

Part 2

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PROCEEDINGS OF THE LINNEAN SOCIETY OF LONDON

153rd Session (1940-1)

Part 2

PROCEEDINGS OF THE GENERAL MEETING ON 6 March 1941

Dr. E. S. RUSSELL, O.B.E., President,
in the Chair

The Proceedings of the Special General Meeting held on Thursday, 7 November 1940, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last meeting :—Exors. of the late T. B. Blow, Mr. A. H. Hamm, Mr. A. W. Rymer Roberts, Prof. F. E. Weiss, Dr. J. C. Willis, Royal College of Surgeons of England, Conservator of Forests, Entebbe, Uganda and the National Library of Wales, Cardiff.

The following Fellows signed the Obligation in the Book of the Charter and Bye-Laws and were admitted :—Kailas Nath Kaul and James Insch.

Certificates of recommendation of the following candidates for Fellowship were read, for the second time, in favour of Bryan Patrick Beirne, Rev. Leslie Walter Allam Ahrendt, James William Matthews and Angus d'Albini Bellairs; for the first time, in favour of Eric Otteleben Callen and William Thomas Williams.

A certificate of recommendation of the following candidate for Associateship was read for the first time,—Thomas Alfred Dymes.

The President reported the deaths of the following Fellows,—Mr. E. R. Gunther, Mr. R. E. Nicholas, Mr. Rudolf Beer, Dr. J. Burt Davy, H.G. The Duke of Bedford, K.G., Miss E. L. Turner, Mr. James Drummond, Mr. Edwin Ashby and Mr. Thomas Bates Blow.

The President announced that General Meetings would be held this year in June and July ; and reminded Fellows that they were invited to make recommendations for new Members of Council and Officers.

The following papers were read,—

JAMES HORNEILL, F.L.S. 'The causation of pearl formation in *Pinctada vulgaris*.' (Dr. G. F. HERBERT SMITH gave an account of it in the author's absence. Discussed by Prof. F. E. Weiss and Mr. I. H. Burkill.) [Printed in full, p. 144.]

Dr. MALCOLM A. SMITH, Sec.L.S. 'The Herpetology of the Andamans and Nicobars.' (Discussed by Brigadier W. H. Evans and Dr. A. S. Corbet.) [Printed in full, p. 150.]

Mrs. C. K. RICARDO-BERTRAM, F.L.S. 'Fishes of the Bangweulu Region.' (In the author's absence Dr. E. TREWAVAS gave the account of it which follows. The paper will be printed in the Journal, Zoology.)

Abstract.—

The Bangweulu region has been defined by Worthington as the whole of the drainage basin of the Luapula River above the Mumbatuta Falls, over which the river falls not long after it leaves the Bangweulu swamps. It is this region that was studied by Miss Ricardo and Miss Owen between July 1936 and February 1937. Their collection of fishes, numbering about six hundred specimens representing fifty-two species, increased the number of species known from the region from fifty-four to sixty-seven, including five not previously described.

Dr. Worthington has stressed the large faunal element which this basin possesses in common with the Zambezi, although it is the source of the Congo, and Captain Pitman has observed the closeness of the headwaters of the two river systems in these swampy uplands, and their temporary intercommunication during the wet season. The new collections emphasize this Zambezi content, which, from previous records, including those of Drs. David and Poll on the Belgian collections, is known to extend also into the upper Congo waters from the Mumbatuta Falls to below Lake Mweru. There, however, it is outweighed by a richer Congo element. It is once more apparent that the essential homogeneity of the African fish fauna is the result of the common origin of the great river systems in the central uplands, where even to-day a swamp may drain now into one basin now into another according to the season, and where earlier earth movements

and climatic changes must have given even more opportunity for interchange of faunas.

Miss Ricardo and Miss Owen were able to observe the breeding habits of the small species of *Tilapia*, *T. sparrmani*, which inhabits these waters and was conspicuous in a small lake, Lake Young, on the Mansya River, a tributary of the Chambezi. Normally only the smaller individuals are found near the lake-edge and larger fishes, up to 200 mm., are found in the open water. This was the state of affairs when, in September, Miss Ricardo and Miss Owen left for their journey to Lake Rukwa. On their return in November they found that the larger fishes were congregated in the shallows, especially in clear water with a sandy bottom. They had paired, and the pairs had hollowed out circular depressions in the sand, in which clusters of greenish eggs had been deposited. Both parents guarded the 'nest' against all trespassers. Neither eggs nor young were found in the mouth in this species, but fry were found crowded at the extreme margin of the lake and in little pools on the shore.

Other fish were found in breeding condition in this and the following months, which are the hot and wet season in this area, but detailed observations on breeding habits were not made for any other species. Notes were made on the food of the majority of the species captured.

SIR WILLIAM WRIGHT SMITH, F.L.S., and H. R. FLETCHER. 'The section *Soldanelloideae* of the genus *Primula*.' (In the authors' absence, the BOTANICAL SECRETARY read an abstract supplied by them. Discussed by Prof. F. E. Weiss and Dr. J. Ramsbottom.) [To be printed in the Journal, Botany.]

Professor WEISS considered Sir William Wright Smith's suggestion that the pendant bell-like shape of the *Primulas* of the *Soldanelloideae* section might be due to the wet climate of their habitat a good one. Our own cowslip and oxlip had a similar habit, and our climate may be considered a damp one.

The following papers were read in title,—

SIR WILLIAM WRIGHT SMITH, F.L.S., and H. R. FLETCHER. 'New Asiatic *Primulas*.' [To be printed in the Journal, Botany.]

W. HARTLEY. 'New species and varieties of the genus *Eriachne* R. Br. (Gramineae).' (Communicated by A. D. COTTON, F.L.S.) [To be printed in the Journal, Botany.]

THE CAUSATION OF PEARL FORMATION IN *PINCTADA VULGARIS*.

By JAMES HORNELL, F.L.S.

THE much advertised products of the pearl-oyster farms in Japan which masquerade under the name of 'Cultured pearls', are entirely dissimilar in structure to the true Orient pearls produced by various species of pearl-oysters when living wild under natural conditions; they are in no sense comparable in intrinsic value as gems, except in the fallacious criterion of outward appearance. A naturally formed Orient pearl possesses an extremely small nucleus, often, indeed, microscopic; in many instances it consists of calcareous matter, and when this happens its presence may easily fail to be recognized. As a consequence a true natural pearl may be defined as consisting of a solid mass of homogeneous nacre arranged in concentric layers around a minute central nucleus. Conversely, the so-called 'cultured pearl' of Japanese origin if sectioned and examined microscopically is found to consist of a foreign nucleus of such large size as to represent approximately from 90 to 95 per cent. of the total volume and weight according to size. The natural lustrous pearl nacre laid down by the pearl-oyster upon and around this is an exceedingly thin layer, and between this coating and the nucleus—usually a ball of mother-of-pearl—is a thin membranous layer. This intercalated layer represents the first reaction of the treated pearl-oyster to the shock of the operation performed upon it; it is an attempt to mitigate the injury received by the introduction of a large and irritant foreign body into its tissues.

This first-formed layer upon the nucleus has the same origin and constitution as the repair membrane secreted by a pearl-oyster as a first-aid measure when one of its valves suffers damage. During experiments carried out in Ceylon in 1902-3, in which I broke holes of various sizes and shapes in pearl-oyster shells, the molluscs closed the apertures within a few hours by the deposit across them of a film of dirty yellowish chitinous membrane; in it no lime salts were deposited. Only after a further lapse of time did the oysters begin to form a deposit of nacre upon the inner surface of the repair membrane.

From this it follows that in the 'cultured pearl' this layer of repair membrane constitutes a concentric film of weakness; it serves also as a rough and ready means of determining whether a pearl is natural or cultural if the owner be willing to run the hazard involved. If the pearl be natural the application of considerable pressure does not cause bruising, and in Colombo it is a common experience to find a native gem dealer when offering a pearl for sale to invite the prospective purchaser to

stamp upon it to prove that it is genuine. The explanation is that natural pearls are homogeneous in structure and have no plane of weakness such as culture pearls have. Upon these latter, pressure, or preferably a sharp blow, will usually cause the thin coating of nacre, separated from the large nucleus by the layer of repair membrane, to star in the same way that old and dry layers of whitewash upon a wall will crack radially when struck with violence.

The discovery of how to produce 'cultured pearls' is not the solution of the problem of how to induce pearl-oysters to form true or homogeneous pearls by artificial means.

This end I was able to accomplish as long ago as 1908, but before detailing the experiments which led up to final success, it appears desirable that I should place on record a condensed summary of the conclusions to which I have come concerning the varying nature of pearl causation in pearl-oysters living under natural conditions.

These conclusions are the result of a quarter of a century's experience in the field, and of hundreds of experiments during my service with the Governments of Ceylon and Madras, first as Marine Biologist and Inspector of Pearl Banks and later as Director of Fisheries, Madras; the most important results were, however, obtained in 1908 when supervising the operations of the Ceylon Company of Pearl Fishers, Ltd. They modify very considerably the earlier views put forward by the late Prof. Sir William A. Herdman and myself in 1905 ('Ceylon Pearl Oyster Reports', Roy. Soc. Lond. III, pp. 49-65; 1905).

These final conclusions may be summarized as follow:—

(a) *Parasites*. I am now fully convinced that parasitic inducement of pearl formation in *Pinctada vulgaris* is of comparatively rare occurrence, though when it does take place it results in the production of the most symmetric and lustrous type of Orient pearl. Incidentally I should state that I have found that this factor functions in this species only when the larval parasite dies within the tissues, thereby involving discomfort due to decomposition. So long as the parasite remains alive and quiescent no pearl-forming cyst or sac is developed around it.

(b) *Sand grains*. I have found the old theory of sand-grain causation to be the correct explanation in many instances; it is to be considered as a rather more important causative factor than that due to the presence of dead parasitic larvae. Pearls of this kind include a notable percentage of the best quality of spherical pearls.

(c) *Nacre fragmentation*. Numerically a far more prolific source of pearl formation is that due to the irritation caused

by minute fragments of nacre dislodged through muscular strain from the insertion areas of the adductor and pallial muscles on the inner surface of the valves. One of these fragments passing into a muscle causes irritation, and this leads to the immigration to the seat of the trouble of nacre-secreting epithelial cells from the mantle surface. These settle round the dislodged fragment, and begin to multiply and eventually form a pearl-forming cyst enclosing the intrusive body. Such 'muscle-pearls' are very common in the vicinity of muscle insertions and form a notable proportion of the small pearls classed under the name of seed-pearls.

(d) *Concretions*. Lastly we have that curious class of pearls formed through the deposit of nacre around those minute crystalline bodies which Sir W. A. Herdman and I termed *calco-spherules*. These are exceedingly tiny calcareous bodies, spherical or slightly oval in shape, often found in considerable numbers at certain points in the pearl-oyster's tissues. The most common location is in the tissues adjacent to the anterior dorsal corner of the visceral mass. Around many of these bodies pearl cysts are formed by immigration of nacre-secreting cells from the secretory epithelium. When these calco-spherules occur they are usually found in numerous groups; whenever a pearl sac is formed around one, it increases rapidly in size through the deposit of nacre upon it in concentric layers.

Sometimes these calco-spherular pearls remain in their original location, eventually forming a 'nest' of small seed-pearls, closely packed. Through mutual pressure some of their faces become flattened, and in occasional instances two or more may coalesce, thereby forming compound pearls ranging from twins to multiple groups, somewhat after the fashion in which the fruit of the blackberry is built up of drupels. Under certain circumstances calco-spherules, or the pearls arising from them, tend to travel into other parts of the visceral mass; on several occasions I have found nests containing considerable numbers embedded in the digestive gland. A large proportion of these pearls are more or less misshapen, and usually they are small in size. Calco-spherular pearls probably constitute the majority of the seed-class quality, exceeding even the contribution made by muscle pearls.

When these pearls migrate singly or in small numbers, remaining separate, their shape frequently remains spherical and growth is more rapid than when they are in nests. A fair proportion thereby become of sufficiently good quality to be fit to be classed as true Orient pearls because of their size and lustre.

The experiments in the artificial inducement of pearl production which I carried out, and which eventually proved

successful, were based on the outstanding inference deducible from the foregoing facts, namely, that pearls may be formed around any solid body that causes irritation or inconvenience in the tissues of a pearl-oyster. It became clear that there was no necessity for the object to carry with it on its entry into the tissues some of the epithelial cells from the exterior of the mantle; causation by calco-spherules arising *within* the oyster's own tissues proved that. Immigration of cells from the epithelium to the inconvenient body, with subsequent cell multiplication, could of itself be relied upon to invest the object with a nacre-secreting pearl sac.

My first experiments based upon this line of attack were made in 1908 on captive pearl-oysters kept in wire-net cages suspended overside from the Pearl Inspection depot ship when lying in Colombo harbour. I tried several methods of introducing sand grains and other foreign particles into the mantles of the molluscs. The one that proved most successful was carried out as follows. A number of oysters were taken from the sea and placed dry upon a bench; the warmth of the air and removal from their home in the water soon caused one to open its valves; a gag was slipped at once between them. When several pearl-oysters had been thus gagged open, the edge of the mantle was carefully raised successively in each at the most convenient point, and a few grains of sand pushed in as far as possible between the mantle and the shell. This done, the mantle was pressed down upon the grains with a view to drive them into the tissue of the mantle. In other experiments the particles were pressed into the mantle from the inner side. As the operation upon each oyster was completed, the gag was removed and the oyster replaced in sea-water. Later, all were returned in their cage to the sea.

At the end of four weeks the experiment had to be terminated owing to an urgent call to proceed to Madras to take up a new appointment. The results, however, were eminently satisfactory, for out of the small number of oysters treated on this occasion I obtained six perfect spherical pearls lying free within the tissues of the mantle flaps and unconnected with the nacre of the valves. In addition, a considerable number of others were cemented to the inner surface of certain of the valves after the fashion of the well-known joss figures inserted in freshwater mussels by the Chinese. With regard to the true spherical pearls of Orient quality that were contained in pearl sacs within the tissues, it appeared immaterial whether the foreign bodies were introduced into the mantle from the outer or the inner surface of the mantle; the vitally important condition was that the bodies should pass completely through the epithelial layer and become embedded in the connective tissue beneath.

Of the batch of small free pearls obtained in this first successful experiment I handed four of them, together with an account of the method pursued, enclosed in a sealed envelope, to the late Dr. B. Daydon Jackson, then General Secretary of this Society, when I was on leave in England in the summer of 1909. The Assistant Secretary, Mr. S. Savage, kindly made a search at my request for this envelope subsequent to Dr. Jackson's death, but unfortunately without success.

For later experiments than the one detailed, owing to the scarcity of pearl-oyster material, the common Indian Unionid, *Lamellidens marginalis*, had to be utilized; it proved an unsatisfactory alternative. I had, however, no difficulty in inducing the production of an inferior type of pearl by introducing small foreign bodies among the muscle fibres of the posterior adductor. Within three months the great majority of these objects became coated with a substantial coating of nacre. Unlike the smooth-surfaced lustrous pearls formed within the mantle of pearl-oysters after treatment, those produced by *Lamellidens* were more or less wrinkled on the surface, a result brought about by the pressure of the muscle fibres surrounding them during their formation. Here again the origin of the formative pearl sac is to be sought in the immigration of nacre-secreting cells from the epithelial layer.

It was as a result of the successful issue of these experiments that I drew up detailed proposals for the establishment of a 'pearl-farm' on the Indian coast, where practical effect on a commercial scale might be given to the procedure envisaged. The scheme recommended the acquisition of a suitable site and the construction there of a Biological Station and of a working laboratory where the practical operations incidental to pearl inducement should be carried on. This was submitted to the Government of Madras in 1913, at which time the late Lord Pentland was Governor. He was keenly interested in the proposals and exerted his influence to ensure their acceptance. Early in 1914 sanction was accorded by the Government; Krusadai Island, a reef island at the southern entrance to Pamban Pass, at the western extremity of Adam's Bridge, was purchased from the Raja of Ramnad and building operations began shortly afterwards.

Unfortunately, before these were completed, the war of 1914-18 broke out and the ensuing necessity to conserve financial resources caused the preparations to be suspended indefinitely. Even opportunity to extend the experiments was denied, owing to the increase of administrative duties, lack of material and various preoccupations. On my retirement in 1923 I still cherished hope of being able to see my scheme adopted elsewhere, but one disappointment followed

another and nothing eventuated, mainly owing to the widespread impression that Japanese competition is unassailable, in spite of the fact that my method produces true Orient pearls of precisely the same structure and quality as the best naturally produced ones, whereas the Japanese 'cultured pearls' are deceptive personations, like the ass in the lion's livery.

Under these circumstances it appears desirable that I should place on record the final conclusions to which I have come concerning the origin of natural pearls in the pearl-oyster of India and Ceylon, together with a condensed account of the results of my experiments in pearl inducement.

It is of interest to remember that this subject at one time occupied the attention of the illustrious naturalist whose work forms the foundation of systematic Zoology, and that it was principally for the success which Linnaeus had in inducing pearl formation by a method allied to that practised by the Japanese for the production of attached or blister pearls, that the Swedish king ennobled him. For this reason it is appropriate that I should submit the present note to the British Society founded in his honour.

Discussion.—

Professor F. E. WEISS said that he had been interested in Mr. Hornell's communication on the nature of pearl formation in *Pinctada* as some so-called pearls were produced apparently by a pathological stimulus in coconuts. In some of the latter, called blind nuts, the embryo is not formed, and a degenerative change takes place at the point where the embryo would normally be found. This leads to the formation of a pearl-like concretion of carbonate of lime. These vegetable pearls are extremely rare and are highly prized by the Malays.

Mr. I. H. BURKILL endorsed Professor Weiss's remarks, saying that coconut pearls are concretions of calcium carbonate formed under the eyes of the shell when for some reason the radicle of the embryo plant is 'blinded'. The cause is altogether obscure; but there are blinded nuts in great numbers without coconut pearls. It would seem that certain races of the palm are more liable to produce them than others, since they are not produced in certain countries, e.g. Ceylon. The supply of these pearls in Malaysia is absorbed by a demand for talismans in native medicine. The 'Dictionary of the Economic Products of the Malay Peninsula', article 'Cocos', p. 613, supplies references to the literature.

THE HERPETOLOGY OF THE ANDAMAN AND NICOBAR ISLANDS.

[With 2 Maps]

By MALCOLM A. SMITH, F.L.S.

THE Andaman and Nicobar Islands form part of a range of submarine mountains extending southwards from Cape Negrais in the Arakan Yomas, Lower Burma, to Achin Head in Sumatra.

The geological composition of the Andaman Islands, which is Early Tertiary or Late Cretaceous, is like that of the Arakan Yomas; the formation of the Nicobars resembles that of the SW. coast of Sumatra and S. Java. The sea that separates the Andamans from Burma is a comparatively shallow one, being generally not more than 50 fathoms deep. As pointed out by Sewell, however, this shallow sea has arisen partly by the deposition of land detritus, and at one time the Andaman Sea extended much further to the North. Between the Nicobars and Sumatra there is a much deeper channel, and this deep sea extends northwards between the Islands and the mainland of Asia as far as Lat. 13°. From it emerge Narkondam and Barren Island, which are volcanic in origin. The latter was in active eruption some 45 years ago, and is not yet quiescent. The islands are densely wooded; round them all are extensive coral reefs; their climate is much like that of the adjacent mainland at the same latitude. The most recent view concerning the origin of the Islands has been expressed by Sewell, and the following is an extract of his remarks:—‘The Andaman Sea basin made its first appearance about the commencement of the Tertiary Epoch, when the great alpine Himalayan system began to arise. Simultaneous with the formation of the parallel ranges of the Burmo-Malayan arc, the westernmost of which appears to have arisen in the Andaman-Nicobar section from the sea bottom, there was formed a shallow water basin into which all the rivers of Southern Burma and the streams on the east side of the Andaman-Nicobar region ranges poured their effluent, and out of which the water escaped through channels between the various Islands into the Bay of Bengal. The elevation of the mountain chain progressed till the height of the ridge attained its maximum at about 9,000 feet above sea-level. At the close of the Tertiary Epoch extensive subsidence occurred throughout the whole area of the basin, but more especially on the east of the Nicobar portion of the ridge . . . Finally, in still more recent times, elevation of the ridge and possibly a further sinking of the trough has occurred.’



MAP 1.—Map of the Andaman and Nicobar Islands. Ocean soundings from Carte Generale Bathymetric Cat. Sc. Prince de Monaco. Dec. 1912.

It is possible, also, that the connection of the Islands with the mainland of Asia is linked up with that of the Sunda Shelf, the origin of which has been studied by geologists in recent years. It is now generally believed that during the Ice Ages the abstraction of water by glaciation lowered the level of the ocean throughout the world, at the period of maximum glaciation by as much as 300 feet (50 fathoms). Sunda Land then emerged, linking up the great islands of Malaysia* with the mainland; with it would have appeared the land bridge connecting the Andamans with Burma (map 2), or perhaps broken by a very narrow channel. With the melting of the ice-caps these lands were once more submerged. This is considered to have taken place at the end of the Pleistocene.

For so small an area, the Andaman and Nicobar Islands are remarkably rich in the variety of their fauna. After excluding the marine turtles and the sea-snakes, many more species of which will no doubt be found, fifty-six species of reptiles, divided among eleven families and thirty-seven genera, have been recorded. The indigenous forms number seventeen, more than 25 per cent. of the total. There are no indigenous genera. Amphibia are poorly represented, a condition due perhaps to the absence of perennial water, for there are but few streams.

That Indo-China, and not Malaysia, was the main source from which the Islands received their fauna is evident from a study of the accompanying list. In column 4 is given the full range of the species, and it is assumed that those that inhabit the Indo-Chinese subregion to-day entered the Andamans by the northern route.

There is, however, a small but distinct—about 10 per cent.—Malayan element, namely, *Calotes jubatus*, *Mabuya rugifera*, *Dibamus novae-guineae*, and the indigenous species *Gymnodactylus rubidus*, *Goniocephalus subcristatus* and *Oligodon woodmasoni*, whose relatives are undoubtedly Malayan, that cannot be accounted for in the same way.

At the same time, in endeavouring to explain the presence of this fauna, it must be remembered that the climatic conditions of the region at the time the Islands were populated may have been very different from what they are now. The true Malayan fauna to-day extends north to between Latitudes 10° and 12°; in previous times it may have reached considerably further north.

Whether the Andaman and Nicobar Islands ever had any recent connection with Ceylon is doubtful. The geckos *Cnemaspis kandiana* and *Lepidodactylus lugubris* have a widespread island distribution, and their introduction may have

* The term includes the Malay Peninsula, Sumatra, Java, Borneo and Palawan.

been due to man's agency. The status of the snake *Boiga ceylonensis* is by no means certain, and I have discussed it more fully elsewhere*. *Bungarus caeruleus*, although agreeing best with the Indo-Ceylonese colour-form, could well have been derived from an ancestor of the Indo-Chinese *B. magnimaculatus*.

Of the snakes, the most interesting species is *Natrix piscator*. Two distinct colour-forms exist, one a large spotted form



MAP 2.—Map of the Sunda Shelf (stippled), based on bathymetric charts.

bearing a resemblance to the Indian race (*piscator piscator*), the other a striped form much like the one found in the Malay Peninsula and Java (*piscator melanozostus*). Neither colour-form, however, entirely agrees with those found on the mainland. Some specimens, also, combine both patterns, being like *melanozostus* on the anterior part of the body and like *piscator* on the posterior part.

* Fauna Brit. Ind. vol. III, Snakes (in the press), for which see also the changes in nomenclature, Nos. 49, 53, 59 in the list, pp. 154-6.

The Pit-Vipers are well represented. Stoliczka, who paid a long visit to the islands, writes concerning them : ' One of the most marked features in the reptilian fauna of the Nicobars and Andamans consists in the great number of *Trimeresurus*, particularly in the Nicobars, where the jungle appears to swarm with them.' In no other area of their range do they show such great variation both in coloration and scalation. It is possible to define three species, but more work, particularly in the field, is needed to determine their precise status.

Undoubtedly the most interesting reptile on the Islands is the Gecko, *Phelsuma andamanense*, for its relatives are not Oriental but Madagascan. The genus appears to be a natural one, easily distinguished by several characters from the other geckonids, and composed of some fifteen species that are closely related to one another. Their distribution, apart from the Andamans, is Madagascar, the Comoro, Seychelles and Mascarene Islands.

There is still much work to be done with regard to the fauna of the Islands. It is unfortunate that the collections now available for study are not more exact as regards the localities from which the specimens come. The term Andamans or Nicobars is wholly insufficient. Many of the forms are confined to single islands only, while some of the smaller islands have not yet been collected on.

List of the Species.

Species.	Andamans.	Nicobars.	Indigenous.	Distribution outside Andamans and Nicobars.
AMPHIBIA.				
1. <i>Bufo melanostictus</i>	+	+	no	Oriental Region.
2. <i>Rana limnocharis andamanensis</i>	+	—	no	Tenasserim *.
3. <i>Rana nicobariensis</i>	—	+	no	Tenasserim ; Malaysia.
4. <i>Rana doriae</i>	+	—	no	Tenasserim ; Malay Peninsula.
REPTILIA.				
Crocodylia.				
5. <i>Crocodylus porosus</i>	—	+	no	Oriental Region. Marine.
Testudines.				
6. <i>Dermochelys coriacea</i>	+	+	no	Marine.
7. <i>Eretmochelys imbricata</i>	+	+	no	Marine.
8. <i>Chelonia mydas</i>	+	+	no	Marine.
9. <i>Carreta carreta olivacea</i>	+	+	no	Marine.

* Not seen by me.

Species.	Andamans.	Nicobars.	Indigenous.	Distribution outside Andamans and Nicobars.
Sauria.				
GECKONIDÆ.				
10. <i>Gymnodactylus rubidus</i> .	+	—	yes	_____
11. <i>Cnemaspis kandiana</i> ...	+	—	no	Ceylon ; S. India ; Sumatra ; Mentawai Is.
12. <i>Hemidactylus frenatus</i> ..	+	+	no	Oriental Region.
13. <i>Gehyra mutilata</i>	+	+	no	Oriental Region.
14. <i>Gecko gecko</i>	+	—	no	Indo-China ; Malaysia.
15. <i>Gecko smithi</i>	+	—	no	Malay Peninsula and Archipelago.
16. <i>Lepidodactylus lugubris</i> .	?+	—	no	Ceylon ; E. Indian Archipelago ; Oceania.
17. <i>Ptychozoon kuhli lino-</i> <i>tum</i>	—	+	no	Indo-China ; Malaysia.
18. <i>Phelsuma andamanense</i> .	+	—	yes	_____
AGAMIDÆ.				
19. <i>Goniocephalus subcris-</i> <i>tatus</i>	+	+	yes	_____
20. <i>Calotes cristatellus</i>	—	+	no	Indo-China ; Malaysia.
21. <i>Calotes jubatus</i>	—	+	no	Java ; Philippines.
22. <i>Calotes versicolor</i>	+	—	no	Oriental Region.
23. <i>Calotes mystaceus</i>	+	?+	no	Indo-China.
24. <i>Calotes andamanensis</i> ..	+	—	yes	_____
SCINCIDÆ.				
25. <i>Mabuya m. multifasciata</i> .	—	+	no	Indo-China ; Malaysia.
26. <i>Mabuya tytléri</i>	+	—	yes	_____
27. <i>Mabuya andamanensis</i> .	+	+	yes	_____
28. <i>Mabuya rugifera</i>	—	+	no	Malaysia.
29. <i>Dasia olivacea</i>	+	+	no	Indo-China ; Malaysia.
30. <i>Lygosoma maculatum</i> ...	+	+	no	Indo-China.
31. <i>Leiolopisma macrotis</i> ...	—	+	yes	_____
32. <i>Leiolopisma macro-</i> <i>tympanum</i>	+	—	yes	_____
33. <i>Riopa boweringi</i>	+	—	no	Indo-China ; Malaysia.
34. <i>Dibamus novæ-guinææ</i> ..	—	+	no	Malay Peninsula to New Guinea.
VARANIDÆ.				
35. <i>Varanus salvator</i>	+	+	no	Ceylon ; Indo-China ; Malaysia.
Serpentes.				
TYPHLOPIDÆ.				
36. <i>Typhlops braminus</i>	+	+	no	Oriental Region ; Africa.
37. <i>Typhlops oatesi</i>	+	—	yes	_____
38. <i>Typhlops andamanensis</i> .	+	—	yes	_____

Species.	Andamans.	Nicobars.	Indigenous.	Distribution outside Andamans and Nicobars.
XENOPELTIDAE.				
39. <i>Xenopeltis unicolor</i>	+	—	no	Indo-China ; Malaysia.
BOIDAE.				
40. <i>Python reticulatus</i>	—	+	no	Indo-China ; Malaysia.
COLUBRIDAE.				
41. <i>Acrochordus granulatus</i>	—	+	no	Indo-China ; Malaysia.
42. <i>Elaphe oxycephala</i>	+	+	no	Indo-China ; Malaysia.
43. <i>Elaphe flavolineata</i>	+	+	no	Tenasserim ; Malaysia.
44. <i>Ptyas mucosus</i>	+	—	no	Oriental Region.
45. <i>Liopeltis nicobariensis</i>	—	+	yes	_____
46. <i>Oligodon woodmasoni</i>	+	+	yes	_____
47. <i>Ahaetulla picta andamanensis</i>	+	—	yes	_____
48. <i>Ahaetulla cyanochloris</i>	+	+	no	Indo-China.
49. <i>Chrysopelea paradisi</i> *	+	—	no	Indo-China ; Malaysia.
50. <i>Lycodon aulicus</i>	+	+	no	Indo-China ; Malaysia.
51 a. <i>Natrix p. piscator</i>	+	—	no	India ; Java.
51 b. <i>Natrix p. melanozostus</i>	+	—	no	India ; Java.
52. <i>Natrix nicobariensis</i>	—	+	yes	_____
53. <i>Boiga ochracea walli</i>	+	+	no	Burma.
54. <i>Boiga ceylonensis</i>	+	—	no	Ceylon ; S. India.
55. <i>Cerberus rhynchops</i>	+	+	no	Indo-China ; Malaysia. Marine.
56. <i>Fordonia leucobalia</i>	—	+	no	Indo-China ; Malaysia. Marine.
57. <i>Cantorina violacea</i>	+	—	no	Indo-China ; Malaysia. Marine.
ELAPIDAE.				
58. <i>Bungarus caeruleus</i>	+	—	no	India ; Ceylon.
59. <i>Naja naja kaouthia</i>	+	—	no	Indo-China.
60. <i>Naja hannah</i>	+	—	no	Oriental Region.
HYDROPHIIDAE.				
61. <i>Laticauda colubrina</i>	+	—	no	Marine.
VIPERIDAE.				
62. <i>Trimeresurus cantori</i>	?+	+	yes	_____
63. <i>Trimeresurus purpureomaculatus andersoni</i>	+	+	yes	_____
64. <i>Trimeresurus albolabris</i>	+	+	no	Indo-China ; Malaysia.
65. <i>Trimeresurus labialis</i>	?+	+	yes	_____

* Based on Stoliczka's figure ; not seen by me.

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Discussion.—

Brigadier W. H. EVANS said :—

A few days ago Dr. Malcolm Smith asked me how many species of butterflies were indigenous to the Andaman and Nicobar Islands. My answer was none, as all the butterflies could be linked up with those occurring in Burma or Malaya either as subspecies or so modified as to be accorded specific rank, more as a matter of convenience than as what might be regarded as indicating truly indigenous species.

Subsequently, with the assistance of Dr. A. S. Corbet, I investigated the question in greater detail. There are 94 species recorded from the Nicobar islands. Of these about 10 are either stragglers from Burma or very doubtful records; 76 are subspecies of species occurring in Burma and Malaya, a few being regarded generally as species; 5 are subspecies of species found in Malaya, but not in Burma. Only 3 do not appear to be represented in Burma or Malaya, though even in these cases it is quite possible that an examination may disclose unsuspected relationships. These three species are a *Cyrestis*, whose nearest apparent relative occurs in Java; a *Cirrochroa* with no near relative, but which is almost certainly likely to prove a highly modified sub-species of a common Burmese species; an *Euploea*, whose nearest relative flies in the Moluccas, and this species alone may prove to be indigenous.

The Andamans with 163 species have apparently a richer fauna than the Nicobars. But it is to be noted that many collections have been made in the Andamans, as well as in the Northern and Central Nicobars; the Southern Nicobars are rarely visited by butterfly collectors, who even then only stay a few days and never get an opportunity to explore the mountainous interior of Great Nicobar, where I am sure

quite a considerable number of species await discovery. All the Andaman species are represented in Burma with one solitary exception, an *Euthalia*, whose nearest apparent relative is to be found in Java.

The Andaman Islands, with the Coco Islands to the north, form a compact faunal area, with the exception of the Little Andaman Island to the south, where slight modifications are noticeable. The affinities are definitely Burmese, and I have always regarded the Andamans as an extension of the Arakan Yoma range.

The Nicobar Islands constitute three allied, though sharply marked faunal areas. The northern group, consisting only of Car Nicobar, displays a slight infiltration from the Andamans. The central group comprises Camorta, Nankowri, Katchall and Tillanchong. The southern group displays considerable modifications: it comprises Little Nicobar, Great Nicobar, Pulo Milo and Kondul. The affinities seem to be Malayan rather than Burmese.

Through the courtesy of Colonel M. L. Ferrar, the Chief Commissioner of the Andamans and Nicobars, I was fortunate in spending two months just 10 years ago in visiting the islands. I am no botanist, but it seemed to me that the Andaman forests generally resembled those I had seen in Burma. The country in Car Nicobar and the Central Nicobars is much more open, while the dense jungles in Great Nicobar resembled what I had seen in Malaya.

Dr. A. S. CORBET said:—

Toxopeus defined Paramalaya as a faunistic unit comprising the islands off the west coast of Sumatra up to and including the Nicobars, and considered it to be more or less equal in value to Neomalaya (Malay Peninsula, Sumatra and Borneo) and Java, these three units constituting the sub-region of Malaysia. While it is true that the Sumatran west coast islands form a distinct but somewhat heterogeneous faunistic unit, it appears very doubtful if the Nicobar Islands have any claim to inclusion in such an area.

During studies of the Malaysian Lycaenid butterflies, entailing examination of over 400 species, I can recall only one case of a Nicobarese species being absent from Burma and yet found in Neomalaya. In this instance *Jamides ferrari* Evans occurs in Malaya and Sumatra as a geographical race differing from the Nicobar form. The very distinct races of *J. celeno* (Fab.) and *J. alecto* (Feld.) from the Nicobars show no close relationship with the forms from the islands off the west coast of Sumatra or from Neomalaya.

PROCEEDINGS OF THE GENERAL MEETING

3 April 1941

Dr. E. S. RUSSELL, O.B.E., President,
in the Chair

The Proceedings of the General Meeting held on Thursday, 6 March 1941, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last meeting :—The Swedenborg Society and Messrs. Frederick Warne & Co., Ltd.

Certificates of recommendation of the following candidates for Fellowship were read, for the second time, in favour of Eric Ottleben Callen and William Thomas Williams.

A certificate of recommendation of the following candidate for Associateship was read for the second time,—Thomas Alfred Dymes.

The following Fellows were elected as Auditors of the Treasurer's accounts for 1940–41 :—Representing the Council—Dr. Anna B. Hastings, Mr. Francis Druce ; representing the Fellows—Mr. D. M. Reid and Mr. J. E. Dandy.

The President reported the deaths of the following Fellows,—Mr. R. Lloyd Griffiths and Mr. H. B. Lacey.

The following new Bye-Law was read for the first time :—

Add to Chapter II the following Section,—

VII. During a period of National Emergency the Council may at its discretion remit in whole or in part the Annual Contribution of any Fellow serving in the Armed Forces of the Crown or in other forms of War Service. The decision of the Council as to what constitutes War Service shall be final. The Fellow whose Annual Contribution is remitted under this Bye-Law shall not be entitled to receive the Publications of the Society during the period of remission.

The following papers were read :—

Sir ARTHUR W. HILL, K.C.M.G., F.R.S., F.L.S. 'The Centenary of the Royal Botanic Gardens, Kew, as a Government Institution : some account of the work of

Kew during the past 100 years.' (Discussed by the President, who conveyed his and the Council's congratulations on the Centenary, Sir William Bragg and Dr. J. Ramsbottom. Sir Arthur Hill replied.)

A. C. GARDINER, M.A., F.L.S. 'Variation in the number of cells per colony of the diatom, *Asterionella formosa*.' (Discussed by the President and Prof. V. H. Blackman.) [Printed below.]

The following paper was read in title :—

I. H. BURKILL, M.A., Sec.L.S. 'The make-up of the flowers of *Ranunculus arvensis* Linn.—a study in evolution of Isomerism in phanerogamous flowers.' [Printed in full, p. 161.]

The President announced that the Council had unanimously awarded the Linnean Medal to Professor A. G. Tansley, F.R.S., F.L.S.

FLUCTUATIONS IN THE NUMBER OF CELLS PER COLONY OF THE DIATOM, *ASTERIONELLA FORMOSA*.

By A. C. GARDINER, M.A., F.L.S.

Observations from three London reservoirs, covering two years, have shown that the mean number of cells per colony of *Asterionella formosa* decreased during any one period of rapid multiplication; this regular shift was found both in spring and summer. At the start of a period of growth, colonies with 8–16 cells were commonly encountered; such large colonies were rarely found later in the same period of growth.

Thus, on 20 February 1940 the mean number of cells/colony was 6.9, with concentration of 523 cells/ml. On 5 March, concentration had risen to 2,640 cells/ml., whilst mean number of cells/colony had fallen to 5.7. Maximum concentration was on 19 March with 14,960 cells/ml., when the mean number of cells/colony had dropped to 3.6. This period of growth came to an end about 2 April, by which time concentration had fallen to 690 cells/ml. and mean number of cells/colony to 2.1. Data from three other growth periods showed the same trend.

During a period of 19 weeks, 15 October 1940 to 25 February 1941, when concentration remained low and roughly constant (*ca.* 87 cells/ml.), the mean number of cells/colony, whilst fluctuating within narrow limits, gave no indication of a regular shift in either direction; the mean number of cells per colony during this period was 6.8.

THE MAKE-UP OF THE FLOWER OF *RANUNCULUS ARVENSIS* LINN.—A STUDY IN EVOLUTION OF ISOMERISM IN PHANEROGAMOUS FLOWERS.

BY I. H. BURKILL.

As likely to throw light on laws that underlie the composing of cyclic flowers I became interested, in 1895, in the meristic relations of calyx, corolla, androecium and gynoecium of *Ranunculus*, and I carried out observations, using *R. arvensis*, until my work was interrupted by a change of residence which completely prevented me from cultivating this little annual. On putting the work aside I published my data in the 'Journal of the Asiatic Society of Bengal' (vol. LXXI, part 2, pp. 93-118; 1902)*, as they already afforded some light on the meristic make-up of the flower. A measure had been taken of the degree in which the calyx, with its approximately fixed upper limit of five sepals, is likely to achieve its full complement. The corolla was shown to have a less abrupt upper numerical limit. The androecium and gynoecium were shown not to have an abrupt upper numerical limit, but the carpels to be more controlled in number than the stamens. And, whereas each of these four categories exhibited an individualism in meristic variation, a common underlying influence could be detected in their correlations. The flowers had been found to be most male (if sex be measured by the proportion of stamens present to carpels present) at the commencement of flowering; and attention was drawn to the displacement of petals by stamens.

Thus far the choice of subject seemed justified, but the object had not been attained. I had used seed from various sources, and I had learned that my German sources provided a race differing from my British plants in the make-up of the flowers.

In 1931 Professor E. J. Salisbury referred to my data in a paper entitled 'On the morphology and ecology of *Ranunculus parviflorus*' (Ann. Bot. XLV, p. 556), adding all my totals together in a search for a tendency towards whorls of threes; but I think it was incautious to add them.

In 1927, that is four years before I was aware of his work, I had taken seed of a single plant of *Ranunculus arvensis* from a corn-field near Leatherhead, Surrey, hoping to renew my studies, and had commenced to cultivate a few plants yearly in my garden, using only its progeny, so that I should not suffer from mixed material. I sowed the seed in 1928 and

* I avail myself of this opportunity to correct a series of printer's errors on p. 102 of this paper: in the column headed '6' read 167 for 67, 117 for 17, 36 for 116 and 3 for 33.

repeated the sowing yearly to 1934. I did not self the flowers, but I made sure that my plants were adequately isolated, i.e. that foreign pollen could not be expected to reach them. Moreover, the knowledge that *R. arvensis* is self-pollinated and self-fertile was reassuring (see Knuth, Handb. d. Blütenbiologie, II/1, p. 31 ; 1898). In 1935 I was away from home, but I was able to keep my pure line in cultivation in a garden within the town of Paignton, Devon, where the isolation was satisfactory. In 1936 I was back again in Leatherhead and, having now the requisite leisure, I sowed a larger quantity of seed than before, filling a bed of fourteen square feet : and as soon as the plants flowered I commenced the examination of every individual flower the bed produced. The data for this paper were thus obtained. My Leatherhead pure-line may be regarded as representing the British or 'Kew' race of my earlier countings, but not necessarily the plant in Britain as a whole, for in May 1894 I had made a quite superficial examination of plants from cultivated land in Essex which were richer in stamens (see Journ. Linn. Soc. Bot. XXXI, p. 235 ; 1895). My plot gave me 5,276 flowers. I had intentionally sowed late and the flowering was late. I desired my plants to hurry into flowering, for when they do that they are less floriferous than if they have been over-wintered. Over-wintered plants, if the soil be rich, may branch from the basal rosette or from near it, and because I sought to get as many individuals under examination as possible, to limit the flowering at the commencement was advantageous. As it was necessary to pluck every flower for examination, the preventing of fruiting prolonged flowering towards the end of the plant's life. The first flowers expanded on 30 June, and flowering continued to the end of September—in all over 87 days.

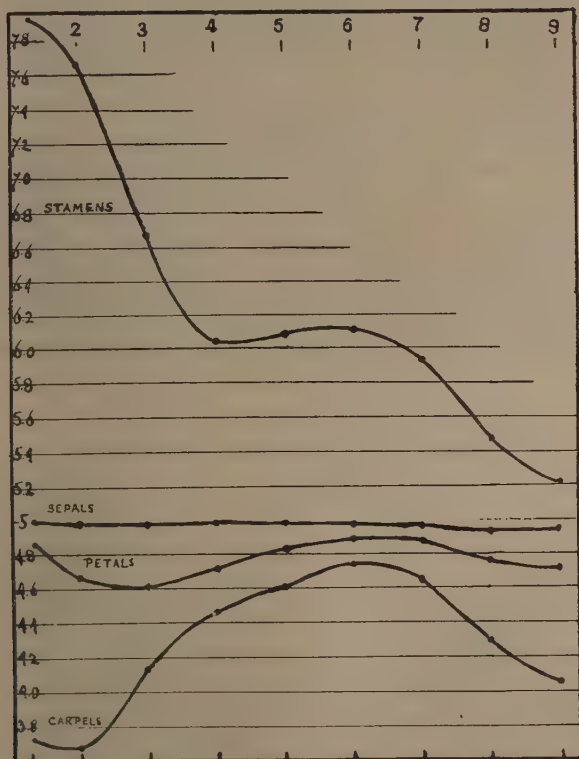
SEASONAL CHANGES IN THE MAKE-UP.

I have divided into periods the 87 days over which the flowering extended, but as no denominator goes into 87, I have been obliged to make one of them shorter than the others ; I have allotted to the first seven days only, leaving 80 to be assigned to eight periods of ten days each. Period by period the number of flowers examined was :—79, 189, 387, 436, 941, 1251, 1302, 499 and 192. Owing to the relative scantiness of the material in the first period, I shall in most of my tables unite it with the second period.

The make-up of the flowers exhibited variation of the same nature as expected from my earlier observations. I give in Table I the mean numbers of organs found, and to bring out the facts which that table exposes I have constructed graph 1 from it.

TABLE I.—The mean number of organs of each category period by period.

Period.	1.	2.	3.	4.	5.	6.	7.	8.	9.
Sepals	5.00	4.99	4.99	5.00	4.99	4.99	4.98	4.95	4.96
Petals	4.87	4.69	4.61	4.72	4.83	4.91	4.88	4.78	4.73
Stamens	7.94	7.66	6.68	6.04	6.10	6.11	5.94	5.49	5.22
Carpels	3.73	3.69	4.16	4.47	4.61	4.76	4.68	4.32	4.07
Total	21.54	21.03	20.44	20.23	20.53	20.77	20.48	19.54	18.98



GRAPH 1.—The meristic variation in the crop, period by period, through flowering (data in Table I).

Table I and graph 1 show how the mean numbers of the organs vary from the beginning to the end of flowering, but

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that a fall may be checked at the height of flowering as if by the operation of a force working like that behind a Grand Period of Growth. In the graph the different categories show strikingly their different meristic behaviour. The sepals varied little. The stamens fell sharply at first, then recovered a little and ended by falling further. The carpels increased in number from the beginning to the height of flowering and then fell. The petals varied in a way intermediate between stamens and carpels, but mostly in agreement with the stamens.

My earlier countings, those of 1895-1900, had been analysed by periods; but the periods were too few—three only in some of the series, and four in others. They had revealed a decrease in numbers of organs per flower towards the end of flowering, but had not revealed any partial recovery at the height of flowering. It may have been that there was none, conditions of cultivation determining it, or it may be that the data were not arranged so as to detect it. In the new data a seasonal change in the variability itself is detected concomitant with the changes in the means: the calculations in support of this are in Tables II and III which give, period by period, the percentages of flowers holding different numbers of stamens and different numbers of carpels. Table IV, gives the Standard Deviation, which is the right index to use for exploring this variability. I have not tabulated the percentages for sepals and petals, as sepals and petals vary too little to make tabulation useful here.

TABLE II.—The percentages of flowers with
13—0 stamens, period by period.

Period.	1 & 2.	3.	4.	5.	6.	7.	8.	9.
Stamens.								
13	0.37	—	—	—	—	—	—	—
12	1.49	—	—	—	—	—	—	—
11	3.73	0.52	—	—	—	—	—	—
10	14.55	1.55	0.23	—	—	0.08	—	—
9	11.94	3.88	1.38	0.85	0.48	0.46	0.40	—
8	25.10	22.22	11.47	13.71	12.87	9.45	2.20	0.52
7	17.54	28.43	17.89	19.87	19.66	16.67	8.22	4.17
6	15.67	24.55	37.16	34.11	37.25	39.40	40.88	30.73
5	7.09	14.99	24.77	26.25	25.26	27.11	36.67	49.48
4	1.87	2.58	4.36	3.40	2.56	4.61	7.82	12.50
3	—	0.77	2.52	1.06	1.76	1.84	3.01	2.08
2	0.37	0.26	0.23	0.43	0.08	0.38	0.40	0.52
1	0.37	0.26	—	0.22	0.08	—	—	—
0	—	—	—	0.11	—	—	0.20	—

TABLE III.—The percentages of flowers with 8—0 carpels, period by period.

Period.	1 & 2.	3.	4.	5.	6.	7.	8.	9.
Carpels.								
8	—	—	—	—	0·08	—	—	—
7	—	0·32	—	1·17	1·28	0·92	—	—
6	0·75	3·88	8·49	10·52	16·31	11·06	5·21	—
5	22·02	33·85	44·04	48·57	47·96	52·23	38·68	26·04
4	36·94	40·83	35·78	30·18	27·03	28·19	42·28	55·21
3	30·60	17·05	10·09	8·18	6·39	6·60	12·62	18·75
2	7·84	2·58	0·92	0·74	0·72	0·69	1·00	—
1	0·37	—	0·23	0·32	—	0·08	—	—
0	1·49	1·29	0·46	0·32	0·24	0·24	0·20	—

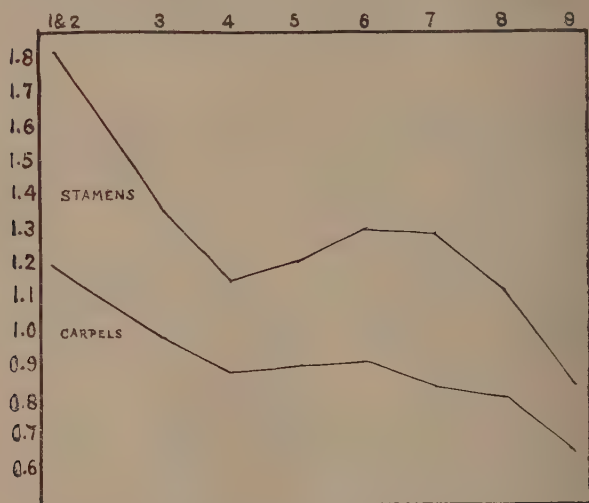
TABLE IV.—The means and the Standard Deviation, period by period, of stamens and carpels, the means of total organs, and the percentage of petaloid stamens in the total number of petals-plus-stamens.

Period.	Stamens.		Carpels.		Total organs.	Percentage of petaloid stamens among petals-plus-stamens.
	Means.	S.D.	Means.	S.D.	Means.	
1 & 2	7·78	1·835	3·70	1·206	21·18	0·59
3	6·68	1·355	4·16	0·998	20·44	1·19
4	6·04	1·154	4·47	0·892	20·23	1·01
5	6·10	1·213	4·61	0·910	20·53	1·12
6	6·11	1·313	4·76	0·926	20·77	0·85
7	5·94	1·301	4·68	0·852	20·48	0·76
8	5·49	1·133	4·43	0·825	19·54	1·56
9	5·22	0·852	4·07	0·665	18·98	1·81

The Standard Deviations from the above table have been plotted in graph 2 in order to bring out vividly that both androecium and gynoecium are most variable at the commencement of flowering and least so at the end, with a secondary maximum in the sixth period.

Observations have been put on record by a few botanists who have interested themselves in differences between early and late flowers. There are my observations in the 'Journal of the Linnean Society' (Bot. xxxi, p. 235 : 1895) showing early flowers richer in stamens than late flowers. In 1894 De Vries published a paper entitled 'Ueber halbe-Galton Curve als Zeichen diskontinuierlicher Variation' (Ber. deutsch. bot. Gesellsch. xii, p. 197 ; see also his 'Mutationstheorie', i, pp. 585 and 591 ; 1901) in which he stated that *R. bulbosus*

var. *sempiternus* is prone to have as many petals, or even more, in its later flowers. In 1910 De Bruyker published a paper entitled 'Voeding en Teeltkeus III—*Ranunculus repens sempiternus*' (Handel. van het XIV Vlaamsch Natuur en geneeskundig Congres te Antwerpen), in which he stated that in this very similar buttercup 'the earliest flowers carried more petals than the latest', alike in the parent plants with which he worked and in the first and second generations of a selection he made for increase of the petals; and his results as shown in his table ii are striking. Salisbury (Ann. Bot. XLV, p. 562; 1931) stated that the number of



GRAPH 2.—The S.D. or σ of stamens and carpels, period by period (data in Table IV).

carpels in *R. parviflorus* varies with the vigour of the plant and the period of flower-production 'affected mainly by the conditions of nutrition'. De Vries also insists on the effects of the conditions of nutrition on the number of the petals in *R. bulbosus*. When he sowed seed in May, the plants whose flowering was delayed until September produced more petals than those which flowered in August ('Mutationstheorie', I, p. 593). The fact is that earliness and lateness are not in themselves causes of difference, but the complex of vigour is, earliness and lateness being part of the complex. Salisbury has expressed this quite correctly. In my experiments with *R. arvensis* the waning of vigour with prolonged flowering

and no production of fruit was made very evident; the vigour waned until death occurred. De Bruyker found manured ground to assist in maintaining high the number of the petals in *R. repens semiplenus*.

During the examination of the flowers of my plants for meristic variation, any morphological abnormalities which were observed were recorded. They were predominately intermediates between petals and stamens. Not a single intermediate between stamens and carpels was met with, and only nine intermediates between sepals and petals, whereas there were 574 intermediates between petals and stamens. All the intermediates between sepals and petals

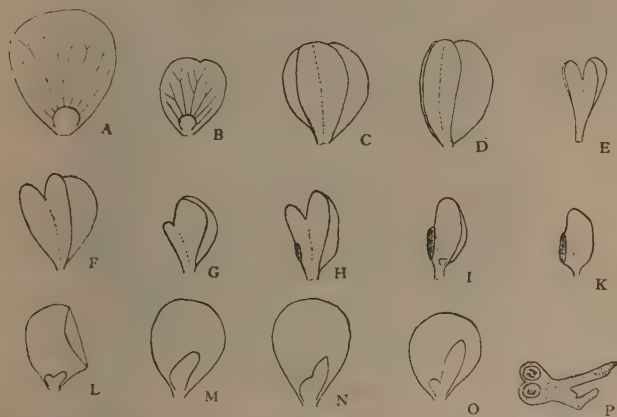


FIG. 1.—A, a normal petal. B, a petal of reduced size, emarginate and slightly asymmetric. C and D, petal-like organs, but with two laminae on each side of a connective, the laminae of unequal size. E, F and G, organs intermediate between petals and stamens without indications of any pollen-sac. H, I and K, similar, but with indication of pollen-sacs. L, M, N and O, petals with the nectarial scale enlarged and oblique. P, a section through an organ like I, showing that the laminae are extensions of anther-lobes. All, except P, are drawn to the same scale, with the half more staminal than the other to the left, though in life it may be as readily to the right.

were sepals with a margin in polish and colour petaloid. The intermediates between petals and stamens were organs such as are drawn in fig. 1. They may be placed in two groups, (i) petals with misshapen nectarial scales, generally asymmetric, and (ii) organs recognizably half petal and half stamen, the petaloid half with a front and a back lamina. I hope to investigate these in greater detail later: here what I need is to insist on their asymmetry.

The nine organs intermediate between sepals and petals were distributed in six flowers, i.e. three flowers held two apiece and three one each.

The 574 organs intermediate between petals and stamens were distributed in 544 flowers, i.e. there were 30 flowers with two each and 514 with one only.

It is impossible to make any statistical use of the scanty intermediates between sepals and petals; but the intermediates between petals and stamens can be used, and in using them it is observed that they became more numerous towards the end of flowering (see the last column of Table IV, where their abundance is recorded as a percentage of the total number of petals-plus-stamens for each period).

By the way it may be stated at once that I shall have cause to use frequently the expression 'petals-plus-stamens', and shall hyphen the words in default of a single word to denote the two categories taken as one. There is no similar disability in regard to stamens-plus-carpels, for they together can be called sexual organs.

THE LEAFY EMERGENCES OF THE MAIN STEM FROM END TO END.

It is essential for my thesis that I should establish the unit value of all the emergences of stem and flower.

When the seed of this little annual germinates, two equal cotyledons appear. One of them is drawn below (fig. 4). They grow to a conspicuous size above the soil, and are shortly joined by a third leaf of ultimately slightly larger size. It pushes itself out between them on one side and parts them until they have lost the appearance of being opposite. Its base creates a sector inserted into the axis. The resultant differentiation involves more than mere increment on that side. As fig. 4 shows, the petiole of the cotyledon is entered normally by three vascular bundles. At the base of the cotyledons the two petioles are connate, making a sleeve within which the plumule is at first sheltered. The sleeve is traversed by five vascular bundles instead of six, i.e. by the two which make the midribs of the cotyledons, by two which are the lateral nerves of the sides of the petioles towards the third leaf, and by the united pair from the other side of the petiole. They unite just below the margin of the sleeve. Fig. 2 is a section through a seedling plant at the formation of the sixth leaf, where the cotyledonary sleeve is seen surrounding the other leaves and its sectorial differentiation is indicated by the distance which separates the lateral cotyledonary bundles on the lower side of the figure in contrast with the proximity to each other of those on the upper side

of the figure ; these latter are the bundles which have a common course, the section cutting them just above their junction. The differentiation extends a little further, for the seedling is sufficiently unilateral for the bundles of the cotyledons to be anchored in the vascular cylinder of the axis at different levels : the lateral free bundles lowest, the midribs next and this united bundle highest. It is not that the slight curvature of the achene is imparted to the embryo when the bundles are laid down, for the embryo eats out a straight cavity for itself in the endosperm ; but the place of the first leaf is prepared before the bundles get their course.



FIG. 2.—A seedling in section at the time of the separation of the sixth leaf after the cotyledons, i.e. the eighth lateral organ of the stem. The sleeve of the cotyledons is outside, with the midribs of the cotyledons to right and to left ; the lateral bundles which do not fuse, are below and those which do, cut just above the fusion, are above. Five sectors have been indicated to show how widely round the axis the bundles of the leaves are dispersed.

With the insertion of the first leaf after the cotyledons between the cotyledons the seedling starts its genetic spiral by unilateral intrinsic activity ; and this spiral quickly becomes stabilized in the leaves which follow at what is commonly called a $\frac{2}{5}$ divergence, and is continued into the flower. I accept the expression 'genetic spiral' as a useful convention and the fractions of divergence as convenient terminology.

Professor Max Hirmer and his pupil Dr. K. Schöffel have published ('*Planta*', xiv, p. 178 ; 1931, and xvii, p. 315 ; 1932) some useful work on this extension of the genetic spiral from the stem of the Ranunculaceae into their flowers.

It is a variable number of leaves which the main axis bears after the cotyledons and before the first sepal. In my cultures the commonest number is eight, or two more than are indicated in fig. 2, and approaching it seven, or one more. The following indicates the usual range :—

Cot/Cot	L	L	L	L	L	flower begins.	Rare.						
Cot/Cot	L	L	L	L	L	L	flower begins.	Not infrequent.					
Cot/Cot	L	L	L	L	L	L	L	flower begins.	Rather common.				
Cot/Cot	L	L	L	L	L	L	L	L	flower begins.	Commonest.			
Cot/Cot	L	L	L	L	L	L	L	L	L	flower begins.	Not infrequent.		
Cot/Cot	L	L	L	L	L	L	L	L	L	L	flower begins.	Rather rare.	
Cot/Cot	L	L	L	L	L	L	L	L	L	L	L	flower begins.	Rare.

Cot=Cotyledon ; L=Leaf.

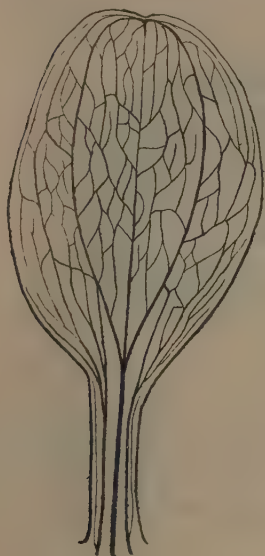


FIG. 3.—The floral diagram of a flower with the formula $K_5C_5A_5G_5$, showing the genetic spiral and five obvious lines of contact or parastichies.

THE COMPOSING OF THE FLOWER.

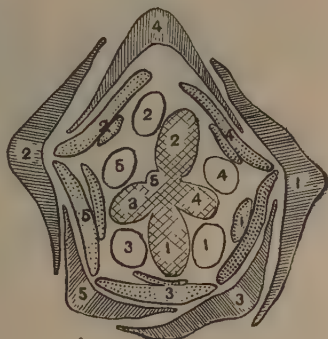
Fig. 5 is a section through a flower-bud with the formula $K_5C_5A_5G_5$, and fig. 3 a floral diagram based on the series of sections whereof that supplying fig. 5 was one. The diagram is composed with the spiral clockwise, but would be true also counter-clockwise : when drawn clockwise, the most obvious 'lines of contact' work against the clock. These are the parastichies and are marked as dotted lines—five in number. The reader must forget what he has probably been told, that the petals alternate with the sepals and the stamens with the petals : they do not, except from adjustment in growth. They become evident, the first petal a little short of the first sepal in such a flower as this, and the first stamen a little short of the first petal and the first carpel a little short of the first stamen, as fig. 3 indicates. Thus all

the first organs of each category are on one parastichy, all the second on another, and so on. It is not easy to see that this is so in an expanded flower; but sections of young flowers must be examined. Fig. 7 is a camera lucida drawing of a bud with the sepals appearing, and fig. 8 a similar drawing with the petals appearing.



4

FIG. 4.—The lamina and free part of the petiole of a cotyledon, $\times 5$. The mesh of the nerves is somewhat finer than that of later leaves.



5

FIG. 5.—A section through a flower bud with the formula $K_5C_5A_5G_5$, the parts numbered by their order of development, outlines drawn under a camera lucida.

In a flower with the formula $K_5C_5A_5G_5$, as in fig. 3, the parastichy running through sepal no. 1 reaches carpel no. 1, but in a flower with the formula $K_5C_5A_6G_5$ passes through stamens nos. 1 and 6 and so reaches carpel no. 5, for the sixteenth emergence in the flower in this case is stamen no. 6, vice the first carpel in the other. It is obvious from this that there is a time when sepals, petals, stamens and carpels do not yet exist, though the emergences which will become them do exist, and that each emergence is the equal of any one of the others, a unit, the visible demonstration of that conception the plastomere.

Professor J. McLean Thompson claims (Publ. Hartley Bot. Lab. 12, pp. 34-43 ; 1934) that very early fusions of emergences occur in the flowers of some species of the Ranunculaceae, notably in *Nigella* in which, as he makes clear, their unit value

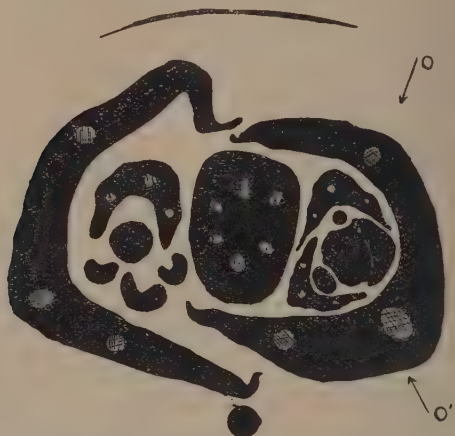


FIG. 6.—A lateral branch in section, showing in the centre the pedicel of its flower and outside, like brackets, its two leaves, each with a branch in the axil. The older branch on the left is cut through the pedicel of its flower, the three lobes of its first leaf and the sheath of its second. The younger branch is cut through its flower at the formation of the first sepal. The leaves of this branch and their axillary buds are seen. The arrows O and O' are explained in the text on p. 179.



FIGS. 7 and 8.—Camera lucida outlines of developing flowers with sepals emergent (7) or with petals emergent (8) ; these are numbered in their order. *s.s.*, the positions of stamens.

becomes obscured ; but fusions do not occur in the flower of *R. arvensis*. Goebel and Professor Salisbury, on the other hand, have claimed very plentiful chorisis in the flowers of Ranunculaceae ; that likewise I do not find in my race of

R. arvensis. And I am convinced that it is right to regard every completed organ in its flower as of unit value for my purpose, each being the product of a single emergence. These units were called 'leaves' by C. M. Wolff ('*Theoria generationis*', 1759) and Goethe ('*Versuch die Metamorphose der Pflanzen zu erklären*', 1790); but it is not right to name them so, though generation after generation of botanists has been encouraged to adopt this over-simplification of the later Nature Philosophers. They are fittingly called emergences so long as they remain indifferent primordia, and this is the term I prefer. The Wolff-Goethe theory equates emergence with foliar primordium: but I must ask the reader to regard the foliar primordium as a stage between the act of emerging and the leaf.

Attempts have been made from time to time to remove the carpel from the conception of being a specialized foliar organ, and I am bound to refer to the last attempt—Abbé Grégoire's. He contributed to the Académie Royale de Belgique (Bull. ser. 5, xvii, p. 1286; 1931) a paper entitled '*La valeur morphologique des carpelles dans les Angiospermes*', in which he claimed that carpels are 'organs sui generis, without homology among the organs of the vegetative equipage', because (i) 'the central part of the axis passes entirely into the construction of the carpels which it is destined to bear', (ii) the carpellary cavity grows as 'a cleft in it', and (iii) the meristem of the carpel-bearing axis is unlike that of a leaf-bearing axis. I am bound to refer to this paper because I do not find the first reason good in regard to the Ranunculaceae. It is true that the axis disappears in most plants; but Troll has suggested some cases in which it does not—*Limncharis*, *Butomus* ('*Planta*', xvii, p. 453; 1932), *Nigella* ('*Planta*', xxi, p. 226; 1933), *Nelumbium*, *Nuphar*, etc. (p. 447; 1933); and in an examination which I have made of *Aquilegia vulgaris* I found what was undeniably the axis to terminate above the carpels. Furthermore, it is well known that the axis does not disappear with the production of the last carpel in *Caltha*, and, turning back to *Ranunculus*, the last carpel is exactly the same as the penultimate carpel or any preceding carpel, with none of which the axis disappears. An imperfect carpel which Grégoire found sometimes in *Aquilegia* seems to me to be comparable with the reduced last follicle seen at times in *Caltha* and the reduced last achene seen not uncommonly in *Ranunculus arvensis*. All are indications that growth is being arrested and the last plastomere of the axis influenced thereby.

Grégoire, unfortunately, did not live to publish a paper he had promised elaborating the views on which, manifestly, he had yet much to state.

The development of the carpel in *Ranunculus* takes place in two stages ; there is the initial emergence, and there is the thrusting of the ovule under and within the cover of the emergence ; so that even the claim that the axis is used up leaves us with an emergence in being before the axis is used up—a unit, beyond contestation the equal at the commencement of its history of the other units in the flower. This unit, after the second phase is over, has its basal growth checked and a constriction inserted which is the equal of the distinct stalk seen under the achene of *R. auricomus*.

THE EMERGENCES OF LATERAL AXES.

Very vigorous plants—plants, for instance, which, germinating in the autumn, vegetate until the following summer—may branch at and near the ground and the branches bear 3-6 leaves ; but all the lateral branches from axils above the base which are spring-produced except possibly, say, two lateral branches toward the base, are two-leaved. Specialization of similar nature is found in other species of *Ranunculus*, sometimes with constancy, sometimes with further distal reduction to one-leaved branches. In some species of *Ranunculus* the lower of the two leaves develops a lateral axis and the upper does not (for some remarks on this see Karl Schumann, 'Neue Untersuchungen u. d. Blütenanschluss,' p. 319; 1890); but in *R. arvensis* both do. Each branch repeats the branching until the vigour for further growth fails.

As fig. 6 indicates, the $\frac{2}{3}$ divergence may be traced from the axillant leaf through the two leaves of the branch into the flower. Karl Schumann wrote of "simultaneous petals," which is wrong, and professed no further interest in the flower-development beyond the production of the first sepal. Goebel also ('Organographie,' ed. of 1923, II, p. 1566) stated that the petals of *Ranunculus* appear together, but he does not name a species. Both botanists seem to have been quoting Payer without verification, or perhaps Schumann relied on observations on teased buds, without the check of sectioning.

Every lateral axis in the way described is much more limited than the main axis. Fig. 6, a section through a lateral branch, shows right and left its two leaves (Vorblätter of German writers), and in the centre the pedicel of its flower. The axillant leaf and main axis are diagrammatic : the rest is from a camera lucida drawing. In the axils of either leaf the tertiary branches are cut, the one through its leaves with their buds, the other, which is cut at a relatively higher level through the pedicel of its flower, through one leaf in its sheath, and through the other above the parting of the lobes. The divergences remain as before.

The reader is now prepared for the statement that the lateral axes which, as has just been recorded, are less variable than the main axis in the number of leaves that they bear, are also less variable in the number and nature of the parts in their flowers. The high index of Dispersion of Variation, or Standard Deviation, for stamens and carpels, recorded in the earlier periods of Table IV, originated in the terminal flowers of the main axis, which, of course, were flowers examined in the earlier periods of flowering. Is it not reasonable to associate the variability in the number of leaves on the main axis with the condition of adolescence? I have evidence of a close relationship between the number of leaves and the total number of parts in the flower, though as yet my data are neither extensive enough for detailed analysis nor can the extension of variability from the axis into the flower be explained clearly yet. It is a variability which, moreover, runs in two channels; for not only are the flowers more variable meristically, but they exhibit a great variable maleness (maleness being measured by the number of stamens). The location of this tendency towards sexual dimorphism in the terminal flowers of the main axis was quite unsuspected when I commenced work, and the discovery of it unwelcome when it came too late to enable me to assign these flowers to a separate count. I had expected a gradual transition from relatively many parts to relatively few, and had not expected the abruptness arising from the lateral branches being so much more organized than the main axis. I was left, however, with this means of analysis—that by eliminating the earlier periods I could eliminate the terminal flowers of the main axes.

These terminal flowers of the main axes appeared to produce a no greater number of petaloid stamens than the later flowers, i.e. they were not more variable in this respect. On the other hand, there is evidence that petaloid stamens result from emergences on relatively less vigorous thalami, as the flowers which held them held rather fewer stamens and rather fewer carpels than the flowers which did not hold them:—

Average number of petals-plus-stamens in flowers:—

Without the abnormalities	11.27
With the abnormalities	10.56

Average number of carpels in flowers:—

Without the abnormalities	4.52
With the abnormalities	4.40

The terminal flowers exercise in a conspicuous measure in starveling plants an inhibition on the development of lateral

flowers ; if they be removed at flowering, the nearest lateral system rapidly develops ; if they be left, and the starvation be near the limit of living, the starveling remains one-flowered.

VASCULAR CONNECTIONS AND SOME POINTS IN THE GROWTH OF THE ORGANS

The vascular tissue of an organ is fitted in amount to the requirements of the organ and an intimate part of it : generally speaking, the larger the organ the more its vasculature. This vasculature can be seen before its need can be demonstrated. *R. arvensis* has the largest achene of its genus, but one of the smallest flowers. The achene is among the most vasculated (Elfriede Rassner in 'Planta' xv, p. 236 ; 1931, and Troll in Ber. deutsch. bot. Gesellsch. LI, p. 217 ; 1934). At the same time the vasculature underlying the organs in the flower exhibits contractions, at least in regard to the sepals.

The passage of three vascular strands between the cotyledons and the axis and between the leaves and the axis has already been illustrated. These cotyledons and leaves have broad bases and the strands are anchored wide apart into the vascular cylinder of the axis (see fig. 2). The sepals have narrower, but still broad, bases, and it is characteristic for them to resemble the leaves in having three vascular nerves passing between them and the vascular network of the axis. In the thalamus of the larger species of *Ranunculus* this network makes a mesh which has been studied by several writers, as Trécul (Compt.-rend. Acad. Sci. Paris, LXXVI/1, p. 795, and LXXVII, p. 402 ; 1873) and G. H. Smith (Bot. Gazette, LXXXII, p. 1 ; 1926, and LXXXV, p. 152 ; 1928). Behind the base of each organ of the flower there is a parenchymatous gap arched over by the mesh. The bundles of the sepals in the larger species of *Ranunculus* are inserted separately into the arches close together ; but the three of the sepal in *R. arvensis* are united at the base and inserted in common. It is only possible to attribute this to want of space. All the organs of the flower above the sepals have no more than a single vascular connection with the mesh. Within the petals the single strand branches fanwise. Within the stamens no branching occurs. Within the carpels the strand forks, one branch reaching the stigma, the other the ovule, and further branches extend later to various parts of the achene. I am not in this place desirous of interesting the reader in the branchings within petals and carpels, but desire that he should keep in mind the fact that, branching or no branching, there is only one vascular connection between the organ and the vascular mesh in the thalamus. It is well to recall that

much in the functioning flower has the most obvious teleological *raison-d'être*. As leaf-bases, for instance, protect the embryonic tissue of the axillary buds, so sepals in the flower protect the later organs, for which purpose a breadth of base is demanded: petals and stamens carry out duties soon over, whereafter a narrow base is advantageous as bringing about but a small wound when they perish: achenes have to be cast adrift and a narrow base is essential. The restriction of vasculature follows the plan of the base and the circumstance of three vascular strands to a sepal and one only to a petal, a stamen or a carpel does not alter the unit value of the unspecialized emergences, and, as I desire to make clear, the plan of vasculature is exposed after the destination of the emergences has been determined. But there is one aspect of the case not without interest, connected with a recognition of vascular strands as paths, certainly sometimes, for hormones, for should the destination of an emergence be subjected to hormonal influences from previously formed organs, the path of the influence would be sectorially restricted when the vascular channel is single and not sectorially restricted when the vascular bundles, as in the leafy part of the stem, are anchored into the cylinder in several sectors. Moreover, even if the cortical tissue between the bundles carries the hormones instead of the bundles, the bundles serve as an index of its amount. There is, one may be permitted to say, a measure of similarity between a sectorial chimacra and a zygomorphic flower, which requires study from this angle.

After vasculature has been initiated, alterations in the directions of growth put shape to the organs, and provide, for instance, a neck for the achene by basal arrest of diametric growth without arrest of elongation, while arrest keeps the bases of petals and stamens narrow.

The growth of the petals in *Ranunculus* suffers another and interesting temporary arrest. After they have been shaped unmistakably they stop growing at the condition seen in fig. 5, touching each other, but not overlapping; they are then valvate, but will become imbricate when growth has been resumed. The resumption of growth is very even all round the margin, as the regularity of the forked—not anastomosed—veins beautifully indicates (see fig. 1 A, on p. 167). In this resumed growth the overlaps which occur are not in every case those expected, but unevennesses in the enlargement of the flower lead to petals which, by the order of emergence, should overlap, having a margin overlapped by a later-formed petal. I have given considerable attention to this overlapping and hope to give more as it is full of

interest because such unexpected overlappings may be used as pointers to indicate alterations of pressure produced in the growth of the thalamus and by the packing of its developed organs. These alterations are posterior in time to the appearance of the emergences, whose unit value for my purpose remains unaltered by them.

It is not uncommon in the expanded flowers of *R. arvensis* for the petals to be unequally spaced; in a five-petalled flower there may be four overlappings and one interval where the two adjacent petals fail to meet. It may be that more than one such interval exists. For the purpose of what I have to record next such flowers must be discarded. Taking flowers where the five overlaps occurred, I have been able to satisfy myself that all the conditions of overlapping illustrated in fig. 9 occur. The normal quincuncial arrangement of the petals is as *R*. An examination of 200 five-petalled side-branch flowers—none of those used in the counts of 1936, but flowers of the same stock available in 1939—suggested that the condition *U* is twice as common as *R* and *T* which is only with much trouble distinguishable from *R*; that *S* is as common as *R*; and *W* half as common. As a cause of displacement unilateral enlargement of the thalamus



FIG. 9.—The normal quincuncial overlap of the petals (*R*), and four ways in which it may be changed during growth; the reversed overlaps are indicated by asterisks.

is suggested on the side of sepal no. 1, and that the reader may follow this he is asked to compare figs. 6, 7 and 8. Fig. 6 shows the two leaves of the limited side-branch, which stand at an angle of about 140° to each other and in the axil of the leaf on the right another limited axis, with its two leaves at a similar angle to each other. Figs. 7 and 8 show these two leaves likewise; and the latter figure shows sepal no. 2 within the angle made by these two leaves and petals nos. 2 and 5 appearing within the sepal. I suggest that delayed enlargement of parts of a flower in this sector may result in petal no. 2 slipping within petal no. 4, giving rise to the condition *S*. The reader will find no other explanation so simple. The condition *U* involves a minimum of two displacements; in it petal no. 1 retains its position, no. 2 slips within no. 4 and no. 3 within no. 5; or there is another possibility, that petal no. 2 has retained its position and no. 1 has

slipped within no. 3, and the opposite edge of no. 3 within no. 5. The latter of these alternatives demands the lesser disturbance because it is confined to what one may define as the first quarter of the clock-face; and, of course, there are also other possibilities. The condition *W* would result from a torsional movement which is by no means impossible, and it involves three displacements. The condition *T* could be derived from *R* by only one displacement, namely of petal no. 3 slipping within no. 5; but I have been unable to find time to ascertain how common it is, owing to the difficulty raised by *R* with the spiral reversed appearing exactly as *T* until one is certain which petal is no. 1 and which no. 2. This, at any rate, is demonstrable, that flower-growth, suffering a check in its course, as in this buttercup, does not end in a constant result. A comparison of figs. 5, 6, 7, 8 and 9 suggests that the slippings occur most often at the places to which the arrows *O* and *O'* in fig. 6 point, i.e. where space between the first sepal and the two leaves of the axis seems to be most free: it is chiefly at that to which the arrow *O* points. But there is much tedious investigation required before anything can be established. Axes in many Angiosperms, I may remind the reader, are well known to change from their original radial symmetry during growth, and Schöffel ('*Planta*', xvii, p. 331; 1932) regarded the petals in *Ranunculus* as 'slipping more or less into the spaces between the sepals'; but he did not go deeper into the changes.

I have serial sections showing the occurrence of the gaps between petals in growing buds at the expected places.

Other species of *Ranunculus* exhibit displacements in the overlapping of the petals: they include *R. parviflorus* (teste Salisbury in Ann. Bot. xlv, p. 551; 1931), *R. bulbosus*, *R. repens* and *R. acris*, for which I have incomplete figures.

It may be remarked that petals in *R. arvensis* are sufficiently differentiated into an up-spiral margin and a down-spiral margin for abnormalities to be staminoid at the former and petaloid at the latter margin, and that such abnormalities can be recognized nearly always to be the last petal or first stamen of the flower. But in the few cases where two petaloid stamens were found in one flower, transition along the spiral from petal to stamen must have been hesitant unless, as seems improbable, the spiral could have been doubled. Here I would remind the reader of Goebel's hesitant *R. auricomus* (Pringsheim's Jahrb. f. wissensch. Bot. xvii, p. 219; 1886).

I have had cause to refer to arrest in the growth of the carpel. It results in the ovule arising actually on tissue not yet emergent from the axis, but about to be emergent: for the ovule appears with the carpel-wall at the back of it in a way which made Lonay (Arch. Instit. Liège, iii, p. 11; 1901) claim it to be in the axil of the carpel. That done,

continuance of emergence lifts the carpel-wall and ovule together; the carpel-wall extends stocking-like over the ovule and the constriction for the neck of the achene is inserted below both. It is interesting to recall that this constriction becomes a stalk in *R. auricomus* and a very conspicuous stalk in *Thalictrum aquilegifolium*.

THE RANGE OF MERISTIC VARIATION IN *R. ARVENSIS*.

The range of meristic variability in the flowers of my race proved to be:—

Sepals,	0 to 7, with Standard Deviation	0.191
Petals,	0 to 7,	0.468
Stamens,	0 to 13,	1.290
Carpels,	0 to 8,	0.932

I do not dispute the possibility that complete absence of organs of one or another of the categories may have originated in some accident. In fact I think insects may have destroyed, say, the sepals in one flower, or, may be, the stamens or the carpels in another, but I trust that the magnitude of my figures and the healthiness of my plants protects me from any error due to accidents.

The flower with the greatest number of parts had the formula $K_5C_5A_{13}G_6$, i.e. it had twenty-nine organs. This number is not the limit possible for *R. arvensis*, but the limit reached in my culture-bed of the year 1936.

There were 193 different combinations, 89 of them represented only by a single flower, 25 by only two flowers, 15 by three flowers, 6 by four flowers and 4 by five flowers, i.e. there were 139 combinations not repeated more than five times. It is of no value to name them. Of the 54 repeated more than five times, 13 were represented by more than 100 flowers, and may be counted normal. I name them in order of abundance.

$K_5C_5A_6G_5$	having therefore	21	organs,	831	flowers.
$K_5C_5A_5G_5$	"	20	"	541	"
$K_5C_5A_5G_4$	"	19	"	493	"
$K_5C_5A_6G_4$	"	20	"	470	"
$K_5C_5A_7G_5$	"	22	"	453	"
$K_5C_5A_8G_5$	"	23	"	273	"
$K_5C_5A_6G_6$	"	22	"	227	"
$K_5C_5A_5G_3$	"	18	"	170	"
$K_5C_5A_7G_4$	"	21	"	155	"
$K_5C_5A_8G_6$	"	24	"	133	"
$K_5C_5A_8G_4$	"	22	"	130	"
$K_5C_5A_5G_4$	"	19	"	110	"
$K_5C_5A_7G_6$	"	23	"	103	"

It is noteworthy that the make-up $K_5C_5A_6G_5$ should have been present in much greater numbers than $K_5C_5A_5G_5$, i.e.

TABLE VII.—The meristic variation in the 5276 flowers.

	0	1	2	3	4	5	6	7	8	9	10	11	12	13
Sepals	1	3	2	13	43	5210	3	1	—	—	—	—	—	—
Petals	1	1	13	148	583	4526	4	1	—	—	—	—	—	—
Stamens	2	5	16	90	220	1379	1863	934	628	75	47	12	4	1
Carpels	21	6	65	534	1719	2362	527	41	1	—	—	—	—	—

TABLE VIII.—Percentages derived from Table VII.

	0	1	2	3	4	5	6	7	8	9	10	11	12	13
Number of organs														
Sepals.....	0.02	0.06	0.04	0.25	0.81	98.75	0.06	0.02	—	—	—	—	—	—
Petals	0.02	0.02	0.23	2.79	11.07	85.77	0.08	0.02	—	—	—	—	—	—
Stamens	0.04	0.09	0.30	1.72	4.36	26.14	35.29	17.70	11.71	1.42	0.89	0.23	0.08	0.02
Carpels	0.04	0.11	1.23	10.12	32.54	44.69	10.10	0.78	0.02	—	—	—	—	—

than the nearest approach to the meristic make-up of a sectorially symmetric flower ; but $K_5C_5A_5G_5$ came second.

It would be unreasonable to suggest that so precise a number of parts as $K_5C_5A_5G_5$ could be arrived at by Natural Selection : that would be attributing a power far too cogent ; but Natural Selection, by acting through the necessity that there be sufficient pollen and ovules for adequate fertility and through any survival values economy of expenditure in tissue may have, would bring the number of stamens and carpels within certain extremes, where other agencies could take up the shaping of the flower itself. I seek to expose the other agencies.

When petals and stamens are added together the number of flowers with each number of the two organs were :— (2) 1 ; (3) 1 ; (4) 1 ; (5) 8 ; (6) 11 ; (7) 35 ; (8) 173 ; (9) 258 ; (10) 1522 ; (11) 1755 ; (12) 799 ; (13) 595 ; (14) 61 ; (15) 41 ; (16) 11 ; (17) 3 ; and (18) 1.

When all the organs are added together the numbers of flowers with each number of total organs were :—(4) 1 ; (5) 0 ; (6) 0 ; (7) 1 ; (8) 1 ; (9) 3 ; (10) 2 ; (11) 2 ; (12) 8 ; (13) 12 ; (14) 14 ; (15) 31 ; (16) 80 ; (17) 176 ; (18) 375 ; (19) 777 ; (20) 1176 ; (21) 1104 ; (22) 843 ; (23) 413 ; (24) 184 ; (25) 58 ; (26) 9 ; (27) 5 ; (28) 0 ; and (29) 1.

As Table VII shows, the sepals varied in a half-Galton curve up to 5, for the scanty number of four flowers beyond may be regarded as abnormalities. The petals also varied in a half-Galton curve up to 5, but less steeply. The stamens, however, varied on either side of 6 and the carpels on either side of 5. I have put all these data into percentages as making them more easy to handle, and give them in Table VIII. A polygon for stamens will be found on a later page (graph 15 on p. 201), and another for carpels (graph 16 on p. 202).

When petals and stamens are added together the percentages of flowers with each number of the two organs become :— (2) 0.02 ; (3) 0.02 ; (4) 0.02 ; (5) 0.15 ; (6) 0.21 ; (7) 0.66 ; (8) 3.28 ; (9) 4.89 ; (10) 28.85 ; (11) 33.07 ; (12) 15.01 ; (13) 11.28 ; (14) 1.16 ; (15) 0.78 ; (16) 0.21 (17) 0.06 ; and (18) 0.02.

When all the organs are added together the percentages of flowers with each number of total organs become :— (4) 0.02 ; (5) 0 ; (6) 0 ; (7) 0.02 ; (8) 0.02 ; (9) 0.06 ; (10) 0.04 ; (11) 0.04 ; (12) 0.15 ; (13) 0.23 ; (14) 0.27 ; (15) 0.59 ; (16) 1.52 ; (17) 3.34 ; (18) 7.11 ; (19) 14.73 ; (20) 22.29 ; (21) 20.92 ; (22) 15.96 ; (23) 7.83 ; (24) 3.49 ; (25) 1.10 ; (26) 0.17 ; (27) 0.09 ; (28) 0 ; and (29) 0.02.

With the above data the reader can realize the nature of polygons resulting.

The arithmetic means and the most prevalent numbers were :—

	Mean number.	Most prevalent number.
Total organs	20.62	20
Sepals	4.97	5
Petals	4.82	5
Petals-plus-stamens	10.92	11
Stamens	6.08	6
Carpels	4.52	5

The prevalent number and the mean number diverge in the carpels.

I have now described the flower of my race of *R. arvensis* as far as direct observation serves. It has (i) a tendency towards maleness at the commencement of flowering, (ii) is more variable meristically then than later, and (iii) this variation is subject to controls differing in effect in the different categories, with (iv) a slight tendency towards the production of organs intermediate between petals and stamens at times when the mean number of stamens is falling most. Its behaviour is consistent with the idea that there is a loss of vigour from the commencement of flowering when the male part of the flower is more favoured than the female, checked at the height of flowering, when the female part of the flower is more favoured than the male.

A later table (XVIII, on p. 211) will show there is expectation that the first, second, third and fourth emergences of the flower will be converted into sepals; that the fifth will also be converted into a sepal unless the vigour of the thalamus is very small when the expectation will be that it becomes a petal; that the sixth, seventh and eighth will be converted into petals, and the ninth also unless the vigour of the thalamus is not enough for the carrying of 16 or more emergences, when it becomes a stamen, and so on, as in the diagrammatic statement on p. 184.

Consider, in illustration of what happens, the thirteenth emergence; if the vigour of the thalamus is so low that no more than fifteen emergences arise on it, there is expectation that it will be a carpel; otherwise it will be a stamen. Or consider the fourteenth emergence, if the vigour of the thalamus does not provoke seventeen emergences or more, there is expectation that it will be a stamen; otherwise it will be a carpel.

Diagrammatic statement showing the probable destination of any emergence in flowers
with 15 to 25 emergences.

Emergence nos. :—															Vigour estimated by emergences.
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
K	K	K	K	K	C	C	C	A	A	A	A	G	G	G	15
K	K	K	K	K	C	C	C	C	A	A	A	A	G	G	16
K	K	K	K	K	C	C	C	C	A	A	A	A	A	G	17
K	K	K	K	K	C	C	C	C	C	A	A	A	A	A	18
K	K	K	K	K	C	C	C	C	C	A	A	A	A	A	19
K	K	K	K	K	C	C	C	C	C	A	A	A	A	A	20
K	K	K	K	K	C	C	C	C	C	A	A	A	A	A	21
K	K	K	K	K	C	C	C	C	C	A	A	A	A	A	22
K	K	K	K	K	C	C	C	C	C	A	A	A	A	A	23
K	K	K	K	K	C	C	C	C	C	A	A	A	A	A	24
K	K	K	K	K	C	C	C	C	C	A	A	A	A	A	25

CORRELATIONS.

It is convenient to collect together into tables the data which are basic to the following pages. I cannot make much use of the sepals, as they scarcely vary. Five tables follow, and are:—petals correlated with stamens, Table IX, which covers all periods; stamens correlated with carpels, Table X, also covering all periods; petals correlated with carpels, Table XI, again covering all periods; petals-plus-stamens correlated with carpels, Table XII, covering all periods; stamens correlated with carpels in periods 4 to 9, Table XIII; and lastly, petals-plus-stamens correlated with carpels in periods 4 to 9, Table XIV.

TABLE IX.—The association of petals with stamens: the number of flowers holding each combination.

No. of petals	1	2	3	4	5	6	Total no. of flowers.	Mean no. of petals in the row.
No. of stamens.								
13	—	—	—	—	1	—	1	
12	—	—	1	—	3	—	4	
11	—	—	—	1	11	—	12	
10	—	1	1	6	39	—	47	4.77
9	—	—	7	13	55	—	75	4.64
8	—	—	15	33	580	—	628	4.90
7	—	1	49	130	753	1	934	4.75
6	—	4	26	220	1612	1	1865	4.85
5	—	2	31	91	1253	2	1379	4.88
4	—	2	9	70	139	—	220	4.57
3	—	2	4	16	68	—	90	4.67
2	—	1	4	2	8	1	16	—
1	1	—	—	1	3	—	5	—
0	—	—	1	—	1	—	2	—
Total no. of flowers ...	1	13	148	583	4526	5	5276	—
Mean no. of stamens in column. }		5.15	6.18	5.95	6.12	—	—	—

TABLE X.—The association of stamens and carpels : the number of flowers holding each combination.

No. of carpels	0	1	2	3	4	5	6	7	8	Total no. of flowers.	Mean no. of carpels in each row.
No. of stamens.											
13	—	—	—	—	—	4	1	—	—	1	—
12	—	—	—	—	3	8	—	—	—	4	—
11	—	—	—	—	16	25	1	—	—	12	—
10	—	—	—	5	25	25	1	—	—	47	—
9	—	—	2	10	25	290	12	1	—	75	4.47
8	—	—	4	31	143	506	136	24	—	628	4.51
7	—	—	10	52	244	894	110	11	—	934	4.93
6	1	3	13	118	597	568	232	5	1	1863	4.73
5	3	—	13	214	548	22	33	—	—	1376	4.66
4	4	1	13	72	107	22	1	—	—	220	4.28
3	3	—	8	29	35	15	—	—	—	90	3.58
2	5	2	2	3	1	3	—	—	—	16	3.53
1	4	—	—	—	—	1	—	—	—	5	—
0	1	—	—	—	—	1	—	—	—	2	—
Total no. of flowers.....	21	6	65	534	1719	2362	527	41	1	5276	—
Mean no. of stamens in column	—	—	5.28	5.45	5.90	6.27	6.76	7.51	—	—	—

TABLE XI.—The association of petals with carpels: the number of flowers holding each combination.

No. of petals.....	1	2	3	4	5	6	Total no. of flowers.	Mean no. of petals in each row.
No. of carpels.								
7	—	—	—	—	1	—	1	4.95
6	—	—	—	2	39	—	41	4.97
5	—	—	1	15	510	1	527	4.92
4	—	—	19	150	2191	2	2362	4.77
3	—	2	61	264	1391	1	1719	4.56
2	—	6	41	131	355	1	534	4.12
1	—	4	17	15	29	—	65	
0	—	—	4	1	1	—	6	
	1	1	5	5	9	—	21	
Total no. of flowers	1	13	148	583	4526	5	5276	—
Mean no. of carpels in the column	..	2.77	3.42	4.00	4.67	—	—	—

TABLE XII.—The association of petals-plus-stamens and carpels : the number of flowers holding each combination.

No. of carpels . . .	0	1	2	3	4	5	6	7	8	Total no. of flowers.	Mean no. of carpels in each row.
No. of petals-plus-stamens.											
18	—	—	—	—	—	—	1	—	—	1	4.82
17	—	—	—	—	—	3	—	—	—	3	4.54
16	—	—	—	—	3	7	1	—	—	11	4.56
15	—	—	—	3	14	23	1	—	—	41	5.01
14	—	—	—	9	18	22	10	1	—	61	4.84
13	—	—	1	19	135	279	137	23	—	595	4.76
12	1	—	2	32	169	470	106	11	1	795	4.77
11	—	1	6	35	538	881	231	6	—	1702	3.73
10	1	1	14	278	638	609	38	—	—	1579	3.55
9	2	1	10	83	118	42	1	—	—	257	2.77
8	5	—	11	59	78	21	1	—	—	175	2.40
7	4	1	8	12	6	4	—	—	—	35	
6	2	2	2	4	2	—	—	—	—	10	
5	3	2	2	—	—	1	—	—	—	8	
4	1	—	—	—	—	—	—	—	—	1	
3	1	—	—	—	—	—	—	—	—	1	
2	1	—	—	—	—	—	—	—	—	1	
Total no. of flowers.	21	6	65	534	1719	2362	527	41	1	5276	—
Mean no. of petals-plus-stamens in each column	(6.34)	—	9.34	9.91	10.69	11.20	11.73	12.46	—	—	—

TABLE XIII.—The association of stamens and carpels in periods 4 to 9 of the flowering: the number of flowers holding each combination.

No. of carpels . . .	0	1	2	3	4	5	6	7	8	Total no. of flowers.	Mean no. of carpels in each row.
No. of stamens.											
10	—	—	—	—	—	—	1	—	—	1	—
9	—	—	—	—	3	8	10	1	—	22	5.41
8	—	—	—	2	66	212	122	23	—	425	5.23
7	1	—	1	21	153	416	96	11	—	699	4.88
6	—	1	2	68	487	788	212	4	1	1563	4.74
5	1	—	8	168	470	516	31	—	—	1194	4.32
4	1	1	12	55	96	20	1	—	—	186	3.66
3	2	—	5	25	29	15	—	—	—	76	3.63
2	2	2	2	3	1	3	—	—	—	13	2.62
1	2	—	—	—	—	1	—	—	—	3	—
0	1	—	—	—	—	1	—	—	—	2	—
Total no. of flowers.	10	4	30	342	1305	1980	473	39	1	4184	—
Mean no. of stamens in each column . . .	—	—	4.20	5.01	5.65	6.12	6.72	7.54	—	—	—

TABLE XIV.—The association of petals-plus-stamens and carpels in periods 4 to 9 of the flowering: the number of flowers holding each combination.

No. of carpels	0	1	2	3	4	5	6	7	8	Total no. of flowers.	Mean no. of carpels in each row.
No. of petals-plus-stamens.											
15	—	—	—	—	—	—	1	—	—	1	—
14	—	—	—	—	1	6	8	1	—	19	5.56
13	—	—	—	2	62	203	124	22	—	413	5.25
12	1	—	—	5	109	390	93	11	—	609	4.99
11	—	—	—	47	439	771	211	5	1	1474	4.79
10	—	1	8	164	522	548	35	—	—	1278	4.34
9	1	—	5	64	99	37	1	—	—	206	3.83
8	1	—	9	48	68	19	—	—	—	146	3.62
7	2	1	7	9	3	4	—	—	—	25	2.96
6	1	—	1	3	2	1	—	—	—	8	—
5	2	2	—	—	—	1	—	—	—	5	—
4	—	—	—	—	—	—	—	—	—	0	—
3	1	—	—	—	—	—	—	—	—	1	—
2	1	—	—	—	—	—	—	—	—	1	—
Total no. of flowers	10	4	30	342	1305	1980	473	39	1	4184	
Mean no. of petals-plus-stamens in each column	—	—	8.40	9.60	10.46	11.05	11.70	12.49			

THE VARIATION STUDIED BY MEANS.

Means have been given in the last rows and the last columns of each of the Tables IX to XIV. Here, in graph 3, to illustrate their use, are two of the series of means plotted across the essential part of Table X; the more or less vertical line shows how the mean number of carpels varied in flowers sampled by the absolute number of stamens present, and the more or less horizontal line shows in a complementary way how the mean number of stamens varied in flowers sampled by the absolute number of carpels.

	G	1	2	3	4	5	6	7
A	10	.	.	5	16	25	1	.
9	.	2	10	25	25	12	1	.
8	.	4	31	143	290	136	24	.
7	.	10	52	244	506	110	11	.
6	3	13	118	597	894	232	5	.
5	.	13	214	548	568	33	.	.
4	1	13	72	107	22	1	.	.
3	.	8	29	35	15	.	.	.

GRAPH 3.—The central part of Table X with the mean numbers of the stamens plotted across it and the mean numbers of the carpels plotted down it.

If a race of *Ranunculus arvensis* could be found in which stamens and carpels were entirely without meristic correlation, all samples drawn by any standards in stamens—it would not matter what—would possess, provided they were large enough to be representative, the same mean of carpels. And conversely, samples drawn by the absolute numbers of carpels would have the same mean of stamens. So, too, with regard to sepals and petals, if no meristic correlation were present. But the means plotted on graph 3 suggest correlations, but that these are complicated; and I use them in the following pages for the purpose of analysing the correlations. A little clearing of the ground is desirable; and for the purpose it is convenient that we command a sample of, say, 2000 flowers of the formulae in the table (Table XV on p. 192) distributed round the mode which is at $K_5C_5A_6G_5$ in the simple way indicated.

TABLE XV. (hypothetical).

Formulae.....	$K_5C_5A_8G_3$ $K_5C_5A_7G_3$ $K_5C_5A_6G_3$ $K_5C_5A_5G_3$ $K_5C_5A_4G_3$	4	$K_5C_5A_8G_5$ $K_5C_5A_7G_5$ $K_5C_5A_6G_5$ $K_5C_5A_5G_5$ $K_5C_5A_4G_5$	6	$K_5C_5A_8G_7$ $K_5C_5A_7G_7$ $K_5C_5A_6G_7$ $K_5C_5A_5G_7$ $K_5C_5A_4G_7$	Total no. of flowers.	Mean no. of carpels.
Dispersion carpels	3	4	5	6	7		
Stamens.							
8	20	40	80	40	20	200	5.00
7	40	80	160	80	40	400	5.00
6	80	160	320	160	80	800	5.00
5	40	80	160	80	40	400	5.00
4	20	40	80	40	20	200	5.00
Total no. of flowers	200	400	800	400	200	2000	—
Mean no. of stamens	6.00	6.00	6.00	6.00	6.00	—	—

The means of this simple hypothetical consortium when plotted by the method used in graph 3 are straight lines intersecting at right angles—at right angles because the plan of the table is rectangular.

From the lower left-hand corner of the statement of formulae, diagonally to the upper right-hand corner, each formula holds one more stamen than carpel. Assuming, as is a reasonable proceeding for illustrating a discussion of *R. arvensis*, that such excess is normal, departure from this excess, correlation being active, will be increasingly difficult with each removal from the formulae on the diagonal line. Discounting the departures according to remoteness at 20, 40, 60 and 80 per cent., arbitrary figures but illustrative, we get Table XVI.

TABLE XVI (hypothetical, derived from Table XV by discounting for remoteness from the diagonal.

No. of carpels . . .	3	4	5	6	7	Total no. of flowers.	Mean no. of carpels.
No. of stamens.							
8	4	16	48	32	20	120	5.40
7	16	48	108	80	32	284	5.23
6	48	108	320	108	48	632	5.00
5	32	80	108	48	16	284	4.77
4	20	32	48	16	4	120	4.60
Total no. of flowers	120	284	632	284	120	—	—
Mean no. of stamens in the column	5.60	5.77	6.00	6.23	6.40	—	—

The manipulation of the figures has caused the means, if plotted as intersecting lines, as in graph 3, to rotate on the mode, closing towards each other as scissor-blades; and from this illustration the reader will appreciate that the angle of intersection at the mode becomes a measure of the closeness of whatever positive correlation there is. It serves my purpose better than any calculation of the Coefficient of Correlation would, because it has more information behind it. The illustration has been made as simple as possible, and the formulae adopted are suggested by the buttercup under study. As the manipulation of the figures has been symmetric about the diagonal, the amount of rotation of either line has been the same; and a slight curvature has been given equally to both which is of no moment as being due to the progression adopted in discounting. It follows that if the discounting had not been symmetric, the lines could have been varied. The means, therefore, if plotted in this way, become sources of information in (i) their angle of intersection, (ii) their departure

from the horizontal and vertical respectively, and (iii) the similarity or dissimilarity of their lengths on either side of the intersection.

Six graphs, one from each of the Tables IX to XIV, are now given side by side. The numerals in circles against the lines indicate the means plotted, thus :—

- 1, means of petals-plus-stamens in flowers sampled by the absolute number of carpels ;
- 2, means of stamens in flowers sampled by the absolute number of carpels ;
- 3, means of carpels in flowers sampled by the absolute number of petals-plus-stamens ;
- 4, means of carpels in flowers sampled by the absolute number of stamens ;
- 5, means of petals in flowers sampled by the absolute number of carpels ;
- 6, means of carpels in flowers sampled by the absolute number of petals ;
- 7, means of stamens in flowers sampled by the absolute number of petals ;
- 8, means of petals in flowers sampled by the absolute number of stamens ;

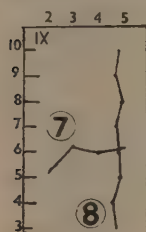
the 12 lines in the six graphs being of eight different kinds of sampling. There are two lines of means of petals (5 and 8) on different samplings ; two of means of petals-plus-stamens, both sampled on the carpels, but covering different periods of time (lines 1) ; three lines of means of stamens on flowers sampled in two ways, the third for a different period (lines 2 and 7) ; and five lines (lines 3, 4 and 6) of means of carpels sampled in different ways or for different periods.

I have made no samplings by sepals, as virtually they have no variation.

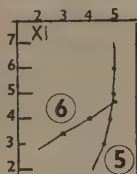
It will be observed that graph 4 is strikingly different from the others. It records the fact that petals and stamens have not the same meristic correlation to each other as have the organs of the other categories, the lines intersecting at right angles. (The drop of the horizontal line towards the left has no importance owing to the fewness of the flowers on which it is based.) In contrast, graph 6 shows that there is a positive correlation between petals and carpels, and graphs 5 and 8 that there is another between stamens and carpels, extending, as graphs 7 and 9 show, to petals-plus-stamens and carpels. Lastly, graph 7 is seen to be more symmetrical than graph 5, and graph 9 than graph 7, indicating that when the early periods of flowering are eliminated a closer correlation is demonstrable.

The variability of the terminal flowers of the main axis has been shown to be greater than the variability of the

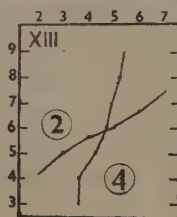
flowers of the lateral axes, and it is this fact which finds expression in the differences between graphs 5 and 8 and between 7 and 9, for the terminal flowers are included in the first of each of these pairs, but excluded from the second. The result of the elimination is that the angle of intersection is reduced from about 64° in graph 5 to about 43° in graph 7; and here follows an interesting observation that when petals-



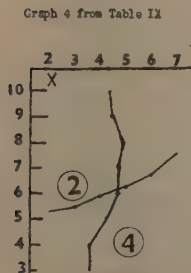
Graph 4 from Table IX



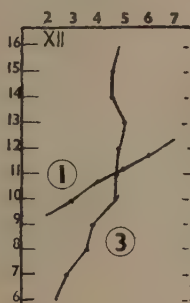
Graph 6 from Table XI



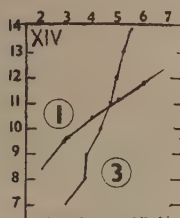
Graph 8 from Table XIII



Graph 5 from Table X



Graph 7 from Table XII



Graph 9 from Table XIV

GRAPHS 4-9, being the means from Tables IX to XIV
plotted as intersecting lines.

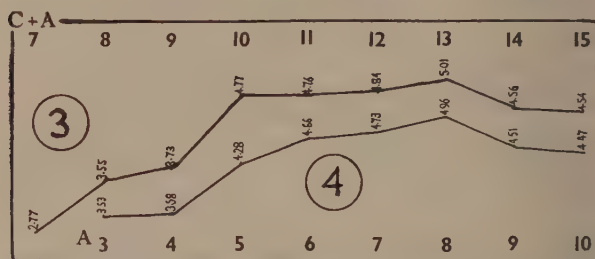
plus-stamens are used for sampling instead of either alone the angle is reduced further, e.g. in graph 9 to about 33° , showing that there is a more intimate relation between the emergences destined to be petals-plus-stamens and those destined to be carpels than between those destined to be stamens and those destined to be carpels. This suggests the following diagram:—

Period in flower-building—C, sterilization
intrudes
Period in flower-building—B, emergences
sexed
Period in flower-building—A, emergences
sexless



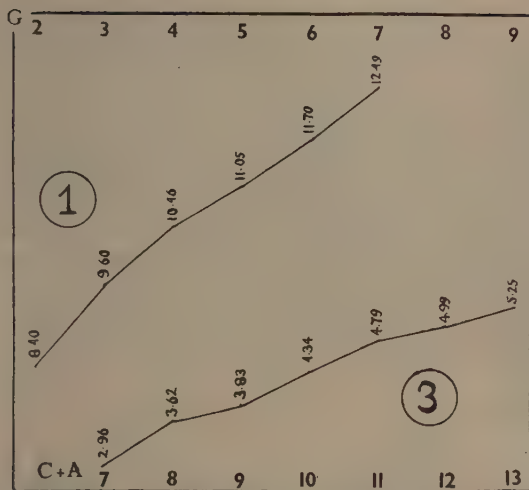
For the purpose of further use of the means, it is well to plot them all from left to right, so that they may be compared easily, keeping the lower terms to the left (graphs 10 to 13.) A commencement may be made by examining the result of plotting the mean numbers of carpels in flowers sampled by the absolute number of petals-plus-stamens: the line so obtained is arched (line 3 of graph 10), i.e., extreme richness in petals-plus-stamens leads towards poverty in carpels.

If the flowers be sampled by stamens only (line 4 of graph 10) the arch still remains, and, therefore, the statement already made that richness in petals-plus-stamens leads towards poverty in carpels can be extended or altered to richness in stamens leads towards poverty in carpels, or, we may say,

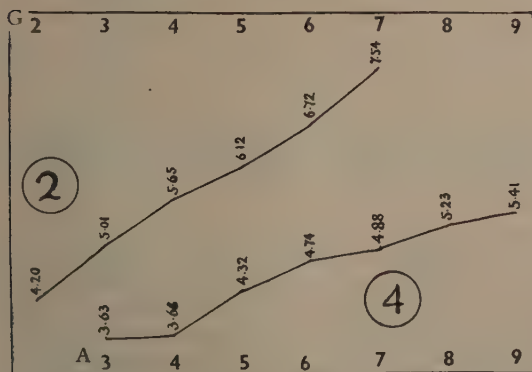


GRAPH 10.—Line 3, means of carpels in flowers sampled by the absolute number of petals-plus-stamens (numbers as the abscissae above) in all periods. Line 4, the same flowers sampled by stamens alone (numbers as the abscissae below). Data in Tables XII and X. The base line of the upper curve is drawn 5 mm. above the lower to avoid overlapping.

leads to an exhibition of a slight tendency towards andro-diclinism. It is not difficult to show, by eliminating the first periods of flowering, that this tendency occurs in the earlier flowers. Line 3 of graph 11 and line 4 of graph 12 give the results of this elimination for flowers sampled by petals-plus-stamens and for flowers sampled by stamens respectively. The elimination removes also the flowers most richly provided with organs, so that whereas line 3 of graph 10 could be extended to 15 petals-plus-stamens, line 3 on graph 11 could not be extended beyond 13: similarly, line 4 in graph 10 could be extended to 10 stamens, but for line 4 in graph 12 the material became inadequate at 9. This slight tendency towards andro-diclinism is therefore connected with the early vigour which favours the production of flowers rich in parts and liberates the variability of the early periods of flowering. It is an influence too slight for detection by any method that I know save analysis by means derived from liberal samples.



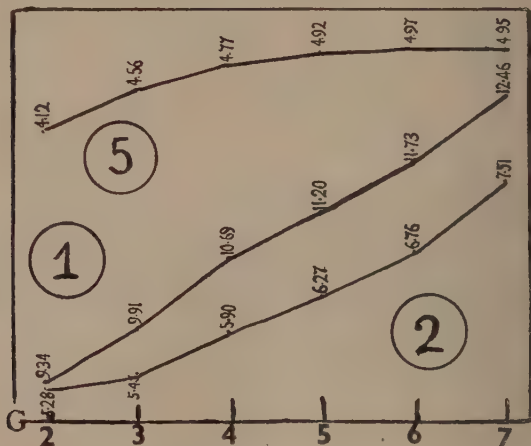
GRAPH 11.—Line 1, the means of petals-plus-stamens in flowers sampled by the absolute numbers of carpels (numbers as the abscissae above) in periods 4 to 9; and line 3, the means of carpels in the same flowers sampled by the absolute numbers of petals-plus-stamens (numbers as the abscissae below). Data in Table XIV.



GRAPH 12.—Line 2, the means of stamens in flowers sampled by the absolute number of carpels (numbers as the abscissae above) in periods 4 to 9; and line 4, the means of carpels in the same flowers sampled by the absolute number of stamens (numbers as the abscissae below). Data in Table XIII.

There is in the genus *Ranunculus* gyno-dioecism grosser than the andro-diclinism, and regarding it several botanists have written; but it has not been observed in *R. arvensis*.

Sagging instead of arching is line 2 in graph 13. It is the line of the means of stamens in flowers sampled by the absolute number of carpels present. Add the petals to the stamens and the line of the means (line 1 of graph 13) is considerably straightened. If the addition of petals causes straightening, the line of the means of petals must be curved compensatingly to line 2, and is found to be so (line 5 of graph 13). Many writers have recognized the petals and honey glands of Ranunculaceae as sterilized stamens, and this to me appears

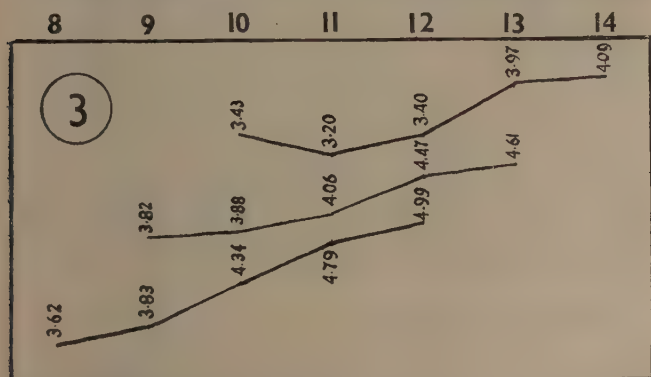


GRAPH 13.—Line 1, the means of petals-plus-stamens in flowers sampled by the absolute numbers of carpels and line 2, the means of stamens alone; line 5, the means of petals alone in the same flowers. Data in Tables XII, X and XI.

undoubtedly true. The detection of this numerical compensation adds proof. Professor Salisbury saw that it occurs in *R. parviflorus* (Ann. Bot. XLV, p. 554; 1931), where it is more obvious than in *R. arvensis*. The differences in numerical relationships between petals and stamens on the one hand and the organs of the rest of the flower on the other hand point also to the relatively recent evolution of the petal.

The utility of the means is yet far from exhausted. To their irregularities I turn, and ask the reader to note the kinks in the lines of the last four graphs. If well established, these kinks indicate something. These kinks occur :—Line 3

of graph 10 at 10 and 13, as if when the absolute number of the petals-plus-stamens is 10 or 13 something in the make-up favours the occasional formation of a carpel or more than one carpel beyond the due proportion; line 3 in graph 11 at 8 and 11, as if when the absolute number of the petals-plus-stamens is 8 or 11 similarly favourable conditions occur in flowers of periods 4 to 9; line 4 of graph 10 at 8, as if when the absolute number of the stamens present is 8 the same occurs, and in contrast the numbers 4 and 7 are unfavourable; line 4 in graph 12 at 4 and 7, as if when the absolute number of stamens is 4 or 7 conditions are unfavourable in the later periods for the carpels; line 1 in graph 13 at 4 with a swing to 7, as if when the absolute number of the carpels is 4 or 7 the make-up favours the occasional formation (here very occasional, as the kinks are minute) of an extra number of petals-plus-stamens; line 1 in graph 11 at 4 with a swing



GRAPH 14.—Mean numbers of carpels in flowers sampled by the absolute number of petals-plus-stamens in three parts of the flowering: above in periods 1 and 2, in the middle in period 3 and below in periods 4 to 9, showing that the kink of the top line at 13 moves to the left.

to 7, as if when the absolute number of carpels in 4 or 7 and flowers only of periods 4 to 9 are under consideration, the same results in minute effect; line 2 in graph 12 at 4 with a swing to 7, as if when the absolute number of carpels is either 4 or 7 the petals are similarly favoured, but occasionally only; line 2 in graph 13 at 4 with a swing to 7, as if when the absolute number of carpels is 4 or 7 the formation of an extra stamen is favoured, but occasionally only.

Three comments arise from this statement:—(i) the lines swing between kinks three units apart; (ii) the kinks are more

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inconspicuous in the lines of the last four entries, i.e., means sampled on the absolute numbers of the carpels, than in the earlier entries; and (iii) between the first and second entry the kinks have moved two points towards the left. This last comment will be investigated at once. Graph 14 has been prepared to explain what has happened, and can be given without its data being necessary. It shows that when the flowers of periods 1 and 2 (combined) are used for obtaining the mean numbers of carpels in samples based on the absolute number of petals-plus-stamens, the plotted line (top line of the graph) has a kink at 13 (such as has been detected in line 3 of graph 10); but when period 3 is substituted the kink has moved to 12, and when the rest of the periods are substituted it has moved to 11. Therefore the shifting of the kink is not unconnected with that conspicuous fall in numbers of stamens shown in graph 1.

It is evident that kinks can represent favourable and unfavourable combinations of organs. We may suppose in illustration that the combination $K_5C_5A_7G_4$ is difficult to realize, whereas the total number of emergences, 21 in this case, is quite easily realized, and that in consequence of the difficulty flowers which should be $K_5C_5A_7G_4$ tend to pass over into $K_5C_5A_8G_3$ or $K_5C_5A_6G_5$: we must assume then that the passing over into $K_5C_5A_6G_5$ will be more readily effected than the passing over into $K_5C_5A_8G_3$ for the reasons which underlie the manipulation of Table XV into Table XVI. On this assumption we may hypothetically transfer from the 48 flowers of formula $K_5C_5A_7G_4$ in Table XVI, four to

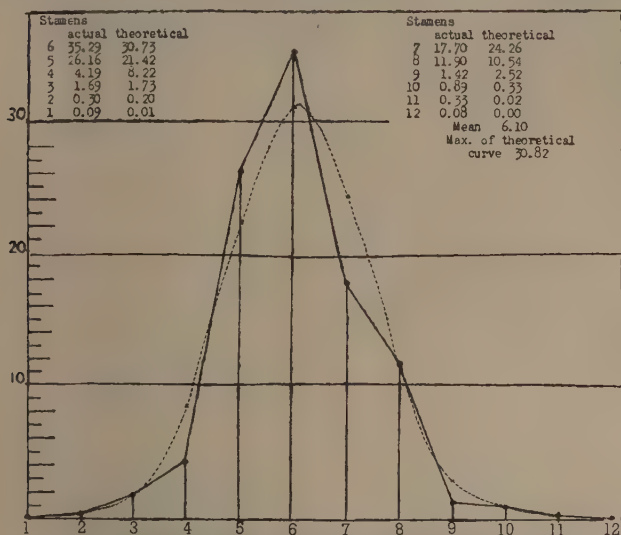
TABLE XVII. (hypothetical, derived from Table XVI by assuming $K_5C_5A_7G_4$ hard to realize).

No. of carpels ..	3	4	5	6	7	Total no. of flowers.	Mean no. of carpels in the row.
No. of stamens.							
8	8	16	48	32	20	124	5.32
7	16	32	108	80	32	268	5.30
6	48	108	332	108	48	644	5.00
5	32	80	108	48	16	284	4.77
4	20	32	48	16	4	120	4.60
Total no. of flowers	124	268	644	284	120		
Mean no. of stamens in each column.....	5.68	5.67	6.00	6.23	6.40		

$K_5C_5A_8G_3$ and 12 to $K_5C_5A_6G_5$, leaving 32. This gives Table XVII.

I do not need to plot the lines, for it is obvious that a kink has been produced; but I proceed at once to seek evidence for favourable or unfavourable formulae in the actual data.

A polygon of the variation in the androecium has been prepared (graph 15), to which my niece, Miss Mary M. Barker, has fitted a 'Normal curve of error'. It shows that flowers with 4 and 7 stamens are in deficit and flowers with 5 and 6 stamens in excess of expectation by amounts which have

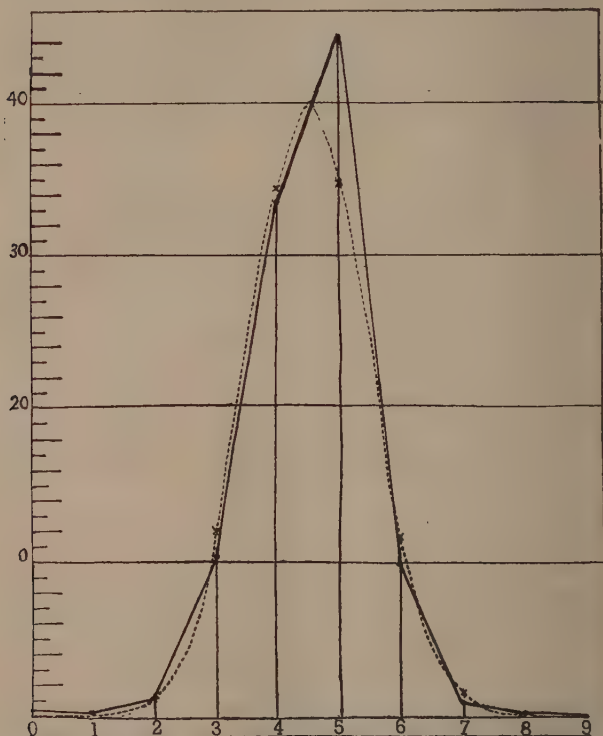


GRAPH 15.—Polygon of variation in the androecium to which a 'Normal curve of error' has been fitted. Ordinates as percentages.

been given on the graph. It is, of course, arbitrary but quite reasonable to use the 'Normal curve of error'. Another polygon (graph 16) follows, giving the corresponding data for the gynoecium. It shows an excess at '5'.

With the aid of Miss Barker I have examined the androecium and gynoecium, period by period. Polygons constructed for each period show an excess in the androecium at 5 stamens throughout, but it is small in the periods 1 and 2 (combined), being 7.09 against an expectation of 6.89; and in period 3 is 14.99 against an expectation of 13.62. After this it becomes conspicuous, i.e., in the periods when the terminal flowers of

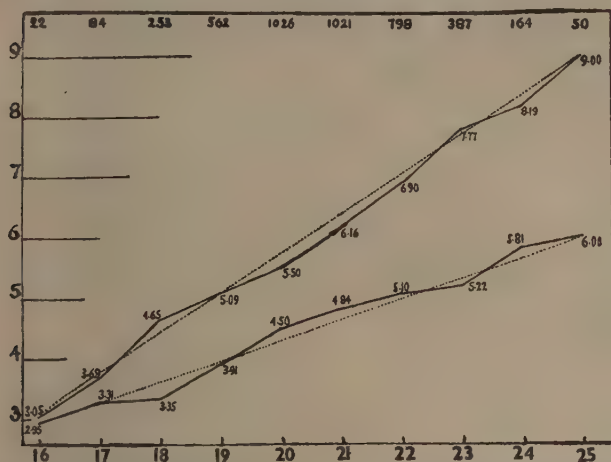
the main axes had ceased to appear. The excess at '6' is as the excess at '5'. The deficit at '4' is conspicuous after the first pair of periods, and the deficit at '7' conspicuous throughout. For the first pair of periods there is a small excess at '10', which is, of course, twice 5, and from it a small secondary mode in the polygon of the androecium for those periods—a suggestive secondary mode!



GRAPH 16.—Polygon of variation in the gynoecium to which a ' Normal curve of error ' has been fitted. Ordinates as percentages.

It is apparent that the formulae with 4 and 7 stamens are worth study; and with this information I devised graph 17 for all flowers with the formulae K_5C_5AxGy . The purpose of excluding all flowers with sepals and petals not five in number was to remove any complications due to correlations between them and the sexual organs. The flowers

left were sampled then by the total number of organs which are the abscissae—the numbers along the base line of the graph. The means of stamens and carpels were calculated and are plotted. Of course, the lower line must be a reflection of the upper. There is a swing of five points on the plotted lines. This does not arise in the pentamery of the flower, although the means have their connection with pentamery, as will be explained. At '18 organs' the dotted lines which I have inserted into the graph suggest ± 4.40 to be the mean for the stamens in association with ± 3.60 for the carpels; but there is in the ascertained means a pull from



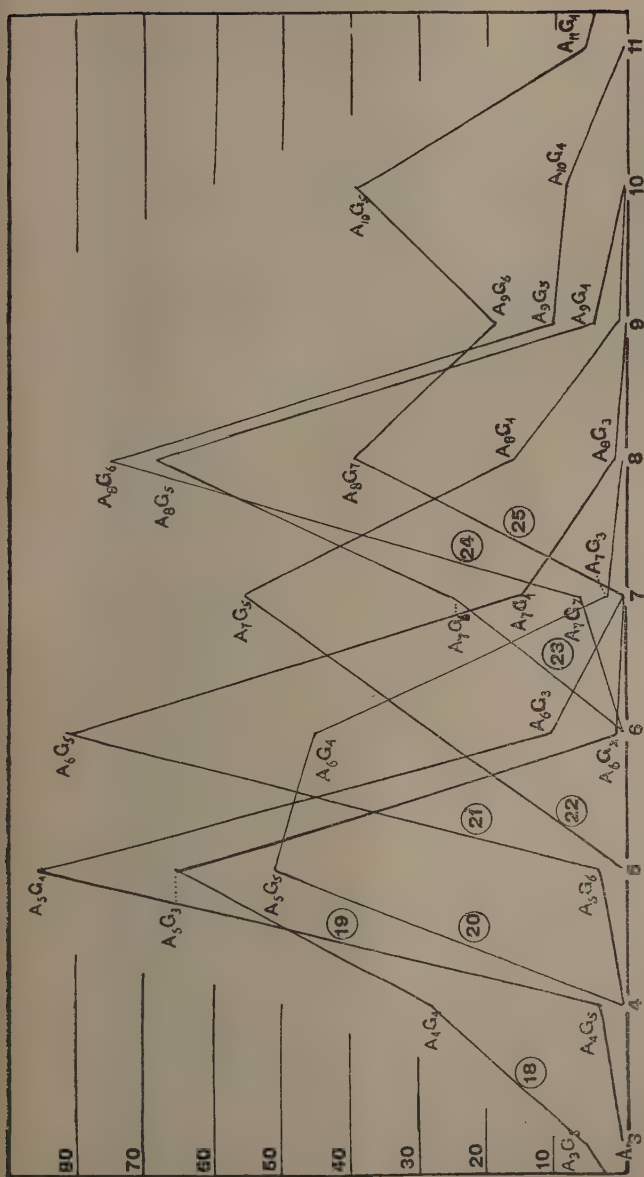
GRAPH 17.—Apportionment of increment to androecium and gynoecium in flowers with 16 to 25 organs. The figures along the lines are the means. The size of the samples is given above.

4.40 towards 5, by which that mean becomes 4.65—a pull such as could be brought about by the increase of the stamens in a small number of flowers at the cost of the carpels. At '19 organs' the favourable '5' is realized in the stamens without much disturbance. At '20 organs' a more or less even pull makes the mean of the stamens 5.50 (6, be it remembered, is a favourable number, as well as 5, in the androecium), and the carpels, for which '5' is a favourable number, reach 4.50. At '21 organs' the pull of the carpels towards realization of their favourable '5' reduces the mean of the stamens towards their favourable '6'. At '22 organs' the gynoecium, now with the expectation of having more carpels than 5, is drawn down towards '5', and at '23 organs'

is still more affected, so that here the androecium obtains a conspicuous excess over expectation. This causes a repetition at what happens at '18 organs', namely, that the plotted line of the means of the androecium is above the dotted line of expectation.

Graph 15 has shown eight stamens to occur, as expected; graph 17 suggests that, as would be expected when the androecium and gynoecium have to share '24 organs', the androecium does not get fully the expected proportion and the gynoecium gets more, expectation being ± 8.35 and ± 5.65 . From these observations I understand that a tendency exists towards isomery which, starting with the calyx, runs through the corolla (see Table VII), building them up to 5, then influences the androecium, building it up to 5, if that is possible, but encountered by the extension of the influence to the gynoecium, where the effort to be isomalous can become antagonistic. The relative simplicity of this suffers interference first in the interlocking of the corolla and androecium, whereby the latter can put in its claim before the former is satisfied, then in the true mean of the androecium being not at '5' but above '6', and in the switch-over from success in achieving isomery of the androecium in less vigorous flowers to success in achieving isomery in the gynoecium in more vigorous flowers, and lastly, in the tendency to andro-diclinism in terminal flowers of main axes. Thus is the flower under competing influences.

I have taken all the flowers used in making graph 17, i.e., none but those with five sepals and five petals, sampled by the total number of organs present—from 18 to 25—and made graph 18. The flowers with '18 organs' had the formulae $K_5C_5A_3G_5$, $K_5C_5A_4G_4$, $K_5C_5A_5G_3$ and $K_5C_5A_6G_2$ in such proportions as to give these percentages—5.49, 27.06, 66.67 and 0.78—which percentages are plotted along the polygon numbered 18 in a circle. All the flowers with '19 organs' are represented in percentages along the polygon numbered 19, and so on. The graph has considerable interest. I take it as undisputed that the number of organs reflects the vigour. When the vigour suffices for 18 organs, most of the flowers have the formula $K_5C_5A_5G_3$. When it suffices for 19 organs most of the flowers have the formula $K_5C_5A_5G_4$. When it suffices for 20 organs most of the flowers have the formula $K_5C_5A_5G_5$. Beyond this a change. When the vigour suffices for 21 organs most of the flowers have the formula $K_5C_5A_6G_5$; for 22 organs $K_5C_5A_7G_5$; and for 23 organs $K_5C_5A_8G_5$, there being now a '5' in the gynoecium. At '24 organs' the prevalent formula has no '5' in the androecium and gynoecium, but is $K_5C_5A_8G_6$. At '25 organs' the polygon has two peaks, one at the formula $K_5C_5A_8G_7$ and the other at the formula $K_5C_5A_{10}G_5$.



GRAPH 18.—Polygons derived from the flowers used in graph 17, one polygon for each sample. Base line, the number of stamens; ordinates, the percentages of the flowers; numbers in circles, the number of organs for that polygon against which it is placed; formulae as regards androecium and gynoecium at the nodes of the polygons.

The reader will find all the formulae in the graph, and by examining it can satisfy himself that alongside the tendency towards isomery is another directing the androecium towards holding one more member than the gynoecium. This pleiometry of the androecium over the gynoecium of 1 occurs in the formulae $K_5C_5A_5G_4$ and $K_5C_5A_6G_5$, which are seen in the graph by their high position to be very favourable combinations, and $K_5C_5A_7G_6$ and $K_5C_5A_8G_7$, which are seen as fairly favourable combinations. Departures from this which intensify the pleiometry become increasingly unfavourable the more they are removed, and the following all occur low down in the graph: $K_5C_5A_6G_3$, $K_5C_5A_7G_4$, $K_5C_5A_7G_3$, $K_5C_5A_8G_4$, $K_5C_5A_8G_3$, $K_5C_5A_9G_6$, $K_5C_5A_9G_5$, $K_5C_5A_9G_4$, $K_5C_5A_{10}G_4$ and $K_5C_5A_{11}G_4$. But $K_5C_5A_8G_5$ and $K_5C_5A_{10}G_5$, though they have marked pleiometry of the androecium, do not occur low down, which circumstance is to be ascribed to the occurrence of '5' in their formulae.

The double-peaked polygon for '25 organs' has one peak where the pleiometry of one stamen is satisfied and one where the demand for isomery (doubled in stamens) is satisfied. It seems to me that a considerable interest lies in this double peak; but it is necessary to call attention to the samples underlying it having been small. It seems not unlikely that the tendency towards andro-diclinism in the early periods arises from the number of stamens being pulled up towards ten, i.e., towards twice five; and, if so, this phenomenon has no direct source in any questions of pollination: no survival needs are involved, and it has nothing to do with securing cross-fertilization, as the old school of flower-biologists would have claimed.

The double-peaked polygon for flowers with 25 organs gives no support to Professor Salisbury's theory of trimerism in Ranunculaceae (Ann. Bot. xxxiv, p. 107; 1920); on the other hand it seems contradictory. But whence arises the three-point swing in the lines of graphs 10-13? It is connected with isomery in fives on one side. Graph 15 shows that the numbers 4 and 7, which are three points apart, are produced in deficit in the androecium. We realize, after what has been written above, that working against the production of '4' in the androecium is the tendency to produce five stamens, and working against the production of '7' is the tendency to produce five carpels, coupled with the tendency towards pleiometry in the stamens. Thus a small number of flowers with vigour, for instance, to produce 18 organs form with the formula $K_5C_5A_5G_3$ instead of $K_5C_5A_4G_4$, and a certain number of flowers with vigour enough to produce 23 organs form with the formula $K_5C_5A_8G_5$ instead of $K_5C_5A_7G_6$, and these transfers increase the means of the carpels when flowers are sampled by the stamens at 4 and 7.

In brief, the three-point swing has nothing to do with successive trimerous whorls although Professor Salisbury's observations on them in *Anemone* are very interesting.

There is a link yet missing in the evidence for this explanation of the kinks, namely, that while the evidence showing how the presence of four or seven stamens favours the carpels has been got from flowers with the formulae K_5C_5AxGy , the plotted means in the graphs 10-13 are based on all the flowers. On that account I have worked out the means for K_5C_5AxGy —flowers extracted from the others and required to answer this break—and have satisfied myself that no discrepancy arises, and I do not need to add more tables in proof.

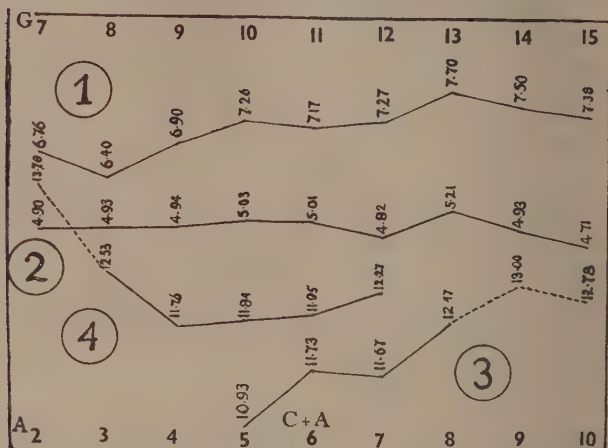
Flowers with seven carpels are few, as Table VII has shown, so few that caution is needed in using them: but flowers with three, four, five and six carpels are plentiful, and the kink at '4' is well demonstrated, if small, in the lines numbered 1 and 2 of graphs 11, 12 and 13. For a line to have a kink upwards at '4' it must fall, or at least not rise, as expected, to '5'. The kink at '4' in these lines arises out of the tendency of the gynoeceium to rob the androeceium in order to complete its own isomery. The reader will observe that the kink is very small.

If it be right that an urge within the axis towards isomery is operative in determining the destination of an emergence at the maleness-femaleness border-line, the urge in this plant operates later in time than the determining according to vigour of the total number of emergences the axis can bear, and the abrupt arrest of the axis with the appearance of the female organs is not a sequel of femaleness but of sexuality, as, indeed, one would suspect, remembering that in Phanerogamic flowers that are purely male the axis may terminate as abruptly. The argument that the gynoeceium is something *sui generis* because the axis disappears with its appearance (see p. 173 above) is converted into an argument that the androeceium and gynoeceium taken together constitute something *sui generis*. And with this the arrest of the growth of the axis is transferred from within the narrow fences of morphology to the wider fields of physiology, where it should be, since 'morphology deals with the stereotyped results of physiology'.*

Having found extremely unfavourable the formulae with the gynoeceium pleiomerous over the androeceium, it is evident that the hypothetical figures in the lower right-hand corner of Table XVIII are far too high to represent *R. arvensis* with any approach to realism. But it is normal in *R. parviflorus* for the androeceium to be meiomerous to the gynoeceium, and I turn to discuss briefly the data Professor Salisbury

* This terse statement is Professor F. O. Bower's ('The Origin of a Land Flora,' p. 7; 1908).

has provided. I have examined these data with considerable care, have tabulated them in various ways and calculated means. I have constructed graph 19 from these means, correcting as far as possible some misprints in his tables which have not proved disturbing. In my graph I number



GRAPH 19.—*Ranunculus parviflorus*: data derived from Professor Salisbury's paper. Lines numbered as in graphs 10–13, dotted if the data considered too meagre. Line 1, means of petals-plus-stamens in flowers sampled by the absolute numbers of carpels (from his table vii, by deducting, first, five for the sepals and then from each total the number of carpels indicated). Line 2, means of stamens in flowers sampled in the same way (his table vi). Line 4, means of carpels in flowers sampled by the absolute number of stamens (the same table). Line 3, means of carpels in flowers sampled by the absolute number of petals-plus-stamens (data extracted as those for line 1).

the lines as in my earlier graphs, and these conclusions emerge :—

(i) there is not the same positive correlation of stamens and carpels as in *R. arvensis*, for line 2, which is of the means of stamens in flowers sampled by the absolute number of carpels, does not rise. Professor Salisbury was aware that the correlation is negative ;

(ii) in flowers rich in carpels it even falls a little in a way suggesting gyno-diclinism ;

(iii) there is a positive correlation between petals-plus-stamens and carpels in the less vigorous flowers, obliterated in the more vigorous flowers by what may be this tendency towards gyno-diclinism ;

(iv) as petals and stamens are vicarious in a remarkable

degree, the numbers of the one increasing at the expense of the other (Professor Salisbury's paper, p. 554), vigour in his plant stifles staminal production by directing stamens into sterile organs, namely, petals; and so, while he claims that the number of carpels can be taken as a measure of the vigour of the axis bearing the flower, so also it can be claimed for the petals;

(v) the vicariousness of petals and stamens leads to a remarkable difference between lines 3 and 4 in my graph 19, which shows that when flowers are sampled by the absolute number of petals-plus-stamens, the means of the carpels rise; but when sampled by the absolute number of the stamens alone, the means of the carpels do not rise but make a downward curve. This curve with more abundant material might be resolved under two influences.

I have commenced observations on *R. parviflorus*; but it will be a long time before I have the data I want. Meanwhile the subject is useful for contrast: it is more floriferous in rich ground than *R. arvensis*, a single plant producing even 150 flowers, and is more difficult to handle.

Professor Salisbury has given a table with the object of demonstrating that vigour stimulates the production of emergences as well as stimulating in close proportions the production of carpels (his p. 566); there is, he says, a 'very high degree of correlation between carpel-production and total emergence-production', but the carpels appear on both sides of his comparison, and the sepals do not vary: so the sepals as being constant do not contribute and the petals-plus-stamens increase with the carpels is as in line 1 of my graph 19. Vigour may be admitted without challenge as influencing the number of organs; the calyx is satisfied out of the number of emergences it permits, i.e., built up to five sepals and no more; the balance is divided between petals-plus-stamens and carpels by influences not working along the lines I trace in *R. arvensis*, and when vigour is abundant that part taken by the petals-plus-stamens exercises or liberates a sterilizing influence. This leads to recalling how commonly vegetative activity delays the flowering of plants.

In my earlier paper on *R. arvensis* I compared its vigour to an estate, and the androecium to a residuary legatee. Arrangements are different in *R. parviflorus*, where the claim of the petals is rarely met to the number of '5', and they get their portion of vigour latest. It is not to be assumed, because petals were the last organs evolved in the angiospermous flower, that this condition in *R. parviflorus* is primitive: on the contrary, this species has probably fallen to proletariat rank, with reduced size, shortened life-period, inconspicuous flowers and early self-pollination from its few stamens.

CONCLUSION.

I have tried to show in the above pages how similar at origin each plastomere in the flower of *Ranunculus arvensis* is to every other one, and have indicated how reasonable it is to regard the emergences as unsexed at emergence. Sex, it must be held, is passed to those that are sexed from the axis which directs one run of them to a male condition and another run of them to a female condition. The axis is successively zoned with vegetativeness (that involves sterility), maleness and femaleness. In *R. arvensis* the number of plastomeres which come within the three zones is variable, with complicated interactions. Although there is known a race of *R. auricomus* wherein petals and stamens are produced in some confusion, I have no knowledge of any disturbance in *R. arvensis* to the succession—sepals, petals, stamens and carpels; and the order of the zones is definite, the sterile organs are emergent earlier than the fertile and the male earlier than the female. But the sterility which spreads over sepals has an up-welling in the axis by which it withdraws the petals from the zone of male-fertility. It is necessary to think of this happening as suggested by the diagram on p. 195, i.e., to think that the male zone after initiation is diminished from below as if the factor in the axis which keeps the sepals from fertility had received an accession of power to overflow. It is not certain by any means that the biochemical condition keeping sepals sterile does overspread the petals; but it looks probable, and at any rate the sterile petals are normally next to the sterile sepals in all angiospermous flowers. Perhaps petals could not have been evolved in any other part of the flower.

The Ranunculaceae happen to afford some of the best evidence available for the view that petals are morphologically sterilized stamens; and it is of interest that I have been able to demonstrate a closer correlation between petals-plus-stamens and carpels than between stamens and carpels, which I take to be an exposure of a briefly established balance between the zones of maleness and femaleness prior to the sterilization of the petals.

The boundary line of this secondary sterilization becomes so fine that abnormal organs are produced more petaloid on the down-spiral side than on the up-spiral side, i.e., the boundary may run right through them, though when this happens neither half is able to attain perfection of its kind.

In my race flowers of the formula $K_5C_5A_6G_5$ proved to be the commonest; and while sepals and petals varied in half-Galton curves, stamens and carpels varied along a Normal Curve of Error, the stamens on either side of '6' and the carpels on either side of '5'.

This is the flower as I understand it:—

Roughly, Natural Selection has shaped and shapes it through the need of sufficient carpels for the next generation, of stamens to pollinate them, of petals to procure pollination between flowers, at least sometimes, and of sepals for protection. Furthermore, leaves enough must exist for food-making. Natural Selection also exercises authority by demanding that all shall work together. Correlations result; but the mechanism of correlation-control is internal to the plant. Botanists in general believe that the cyclic flower so characteristic of the Angiosperms has passed through a spiral phase in its evolution: part at least of the key to understanding how this could be lies in the mechanism of the control of correlations.

Vigour underlies all emergence-production. The following table, which does not contain the most starved and the most

TABLE XVIII.—Means of organs in flowers sampled by the total number of organs.

No. of organs.	No. of flowers.	Means.			
		Sepals.	Petals.	Stamens.	Carpels.
15	34	4.47	3.91	3.94	2.73
16	78	4.92	4.06	4.00	3.00
17	161	4.97	4.31	4.33	3.39
18	375	4.97	4.65	4.96	3.42
19	776	4.98	4.71	5.38	3.93
20	1176	4.99	4.87	5.64	4.49
21	1104	5.00	4.93	6.13	4.84
22	843	5.00	4.97	6.94	5.09
23	407	5.00	4.97	7.78	5.26
24	184	5.00	4.97	8.27	5.79
25	58	5.02	4.98	9.10	5.90

exuberant flowers because of their inadequate numbers, shows that the more the emergences, the higher the means of every category of organs.

Correlation-control is explicable in terms of harmonic activity. It may be that a substance generated in the zone of maleness acts as a stimulant on the development of the zone of femaleness, and that a substance generated in the zones of femaleness reacts, and that, just as auxin in its action on elongation varies with its strength, and even passes over into a retarding body, so the harmonic substances of the generative zones act and react until a balance is struck between the two, with so many plastomeres absorbed into the one and so many into the other. But if this be so, it is necessary to postulate an overruling condition in the flowers of the main axes where stamens are formed in excess. I cannot

suggest why these flowers should exhibit a tendency towards andro-diclinism : all I can do is to point out that the foliage leaves are variable in number on these axes, but not on the lateral axes.

Such harmonic substances as I have suggested may be produced chiefly under the emergences. If they be, their greatest effect will be on organs least removed, therefore along the parastichies which the reader will find inserted into fig. 3. These parastichies are major 'lines of contact'.

Isomery is quite likely to be induced by action along the parastichies, so that flowers approaching isomery are evolved, and, for instance, the flower $K_5C_5A_5G_5$ will be favoured among the variants which fall away from the modal $K_5C_5A_6G_5$.

But a condition of isomery is not necessarily whorled. To obtain whorls there must be a disturbance of the plastochrones ; the series of emergences e.e.e.e.e.e.e must break up into an interrupted succession : K.K.K.K.K—C.C.C.C.C—A.A.A.A.A—G.G.G.G.G, for the study of which *Ranunculus arvensis* seems to have nothing to offer, though it would appear possible to use other Ranunculaceae for aid therein. This one remark may be made, that a survey of the Angiosperms at large suggests that isomery without whorls is unstable.

Moquin-Tandon long ago pointed out that in monstrously fused flowers calyx unites with calyx, and corolla with corolla ; and this is explicable as axis-controlled.

Diplostemony and any meristic arrangement involving multiplications of a basal unit can, of course, be discussed as of parallel evolution.

Professor Salisbury has suggested that the quincuncial calyx of *Ranunculus* is derived from two whorls of three parts and endeavoured to find indications of trimery in my earlier data. I do not find any. What appears in *Anemone* scarcely seems to me an argument for regarding *Ranunculus* as not in fives. On the contrary, what has been deduced above as a possible cause for pentamery in *Ranunculus* may enable part of the trimery of *Anemone* to be interpreted without invoking any ancestry with three-sided apical cells.

In flower-building the abrupt termination of the axis with the last carpel is undoubtedly a phenomenon of great importance. Its evolutionary value is two-fold—the uselessness of escaping beyond the protection of the calyx and the need of the ovules to be freed from competition. It is by inhibition that it ceases elongation, not by a waning or starvation, though the last carpel of *R. arvensis*, as also the last follicle of *Caltha*, may not grow to the same size as the others. This abrupt termination must be controlled from within the axis at an early stage in the establishment of zones with a dominance of sexuality over sterility.

SUMMARY.

A pure line of *Ranunculus arvensis* was procured, a large number of plants raised and the merism of every flower produced examined.

There were found positive meristic correlations between petals-plus-stamens and carpels, petals and carpels, stamens and carpels ; but not the same between petals and stamens.

Sepals varied in number so little that no use has been made of them.

The main axis varied in the number of leaves it bore and had more variable flowers than the invariably 2-leaved lateral axes. But correlation is not established in this paper.

As vigour waned with age, so did variability, but the make-up of the flowers had an excessive maleness on the main axis, which, of course, flowered first.

The object of the undertaking was to seek for indications of the way in which cyclic flowers evolved, and *Ranunculus arvensis* had been selected on account of its approach to isomerism in association with adequate variability.

A tendency towards isomerism was uncovered, and the suggestion is made that organs have their destination determined in the axis by hormones whose effect is greatest as a result of the proximity involved along the major Lines of Contact or parastichies.

This leading to isomery by a force evenly distributed round the axis would not, however, lead to the establishment of whorls. For them a change in the plastochrone is necessary.

The production of flowers in this buttercup occurs in the following stages :—

(i) There is forward growth in an axis about to flower whereby plastomeres are called into existence in numerical proportion to the vigour of that axis ;

(ii) the apical part becomes endowed with fertility, and

(iii) bereft of normal elongation down to a line sharply defined, the level of the lowest sepal ;

(iv) at the same time an inhibition of the normal course of growth towards plastomeres spreads over the very apex ;

(v) the apical part becomes zoned with, in ascending order, sterility, maleness and femaleness ;

(vi) interactions between whatever substance it be that determines maleness and whatever substance it be that determines femaleness establish a balance between the zones of maleness and femaleness, and the sexing of their emergences follows ;

(vii) these substances have or acquire greater power in the neighbourhood of the emergences and, therefore, act most strongly along the Lines of closest Contact or parastichies, and from this a tendency towards isomery results ;

(viii) into the lowest part of the zone of maleness a sterilizing influence enters, causing sterility of a certain number of emergences so that they become petals.

If it be right that substances, say of a hormonal nature, interact between the zones of maleness and femaleness so as to induce that tendency towards isomery which has been detected, it is natural to infer that the isomery of sepals with petals and other instances of isomery are similarly brought about, and that the orderliness of a phanerogamic flower often attributed to close packing arises in no little degree from biochemical interaction.

At this point the flower is made. It grows, and in growth some inequalities develop resulting in displacements of petals. These displacements serve as a reminder that the finished and expanded flower is not merely the morphological composition laid down, but the same with modifications which may be mere pressure-effects, or, as in zygomorphy, may be more. It is in this post-formatinal growth that questions of close packing arise. The Schimper-Braun theory claimed the pressure to appear in the flower at a much too early stage.

If the sterilization of the emergences which become petals is due to an up-welling of the factor of sterilization spread over the sepals, the evolution of petals had its natural position between sepals and stamens, and this observation leads to the following thought. Petals having been called into existence, entomophily set Natural Selection to work in fixing their occurrence, their sizes and their colours, while certain parts of the embryonal tissues which the first flower-visiting insects used as food (see my remarks on *Empis* and *Geranium* in Journ. Bot. 1940, p. 175) became specialized into nectaries for the better preservation of more precious embryonal tissues, including that other honey-gland, the stigma.

In the Ranunculaceae these nectaries developed on emergences of the male zone, as the stigma had developed on emergences of the female zone. But the value of that similarity is not yet to be assessed.

I desire in conclusion to express my gratitude to Miss M. M. Barker for her share in constructing graphs 15 and 16, to Professor J. McLean Thompson for valuable suggestions made on reading my manuscript, and to the Director of the Royal Botanic Gardens, Kew, for facilities given me in the Jodrell Laboratory of the Gardens.

Discussion :—

Dr. V. J. CHAPMAN asked if climate has any effect on the number of floral parts produced, *e.g.* whether a wet period influenced the flowers of a later period.

Mr. BURKILL replied that it was a point which he had not had time to study in view of the great number of observations which were necessary.

PROCEEDINGS OF THE GENERAL MEETING
15 May 1941

Dr. E. S. RUSSELL, O.B.E., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 3 April 1941, having been circulated, were taken as read and confirmed.

The President moved a resolution expressing the Society's very deep regret at the death by enemy action of Mr. FRANCIS DRUCE; gratitude for the many benefits he had conferred on the Society; and profound condolences with his relatives. The resolution was passed unanimously, all standing in their places.

The following were thanked for gifts made to the Library since the last meeting :—Dr. Agnes Arber, Mr. H. H. Bloomer, Mr. W. H. Burrell, Mr. R. J. Flintoff, Mr. W. S. Rowntree, the Royal Meteorological Society and Messrs. Frederick Warne & Co., Ltd.

Certificates of recommendation of the following candidates for Fellowship were read :—For the first time, in favour of Gerald William Thomas Hunter Fleming and Edgar Wolston Bertram Handsley Milne-Redhead.

The following candidates, whose names were read for the third time, were balloted for and elected Fellows :—His Honour H. Drysdale Woodcock, K.C., Bryan Patrick Beirne, Rev. Leslie Walter Allam Ahrendt, James William Matthews, Angus d'Albini Bellairs, Eric Otteleben Callen, and William Thomas Williams.

The following candidate, whose name was read for the third time, was balloted for and elected an Associate :—Thomas Alfred Dymes.

The new Bye-Law, Chapt. 2, Sect. 7, was read for the second time. [For the first reading see p. 159.]

The President announced that the Council had nominated Dr. John Ramsbottom as candidate for election as a Member of Council in place of the late Mr. Francis Druce, whose name they had included in the Ballot List already circulated to Fellows.

[*Text of letter.*]

Doctissimo et Præclarissimo Viro
Domino Matthæo Fabio Medicinæ
Professori Excellentissimo
Marcellus Malpighius

Corporis mei perennis languor continuæq: curæ ita me occupant, ut omnino studijs vacare nequeam; quapropter relictis meditationibus et observationibus summi Pontifici medicinam faciens Amicis meoq: genio haud inseruire ualeo; hinc Vir Doct: me excusatum habeas rogo si ultiores exercitationes circa marinæ pillæ [*sic*] structuram et naturam instituere nequierim. Crudæ admodum sunt meditationes, quas olim tibi communicauim, nec dignæ publica luce. De phosphoro nostro, eiusq: legitima præparatione nil habeo præter ea, quæ a uarijs Auctoribus euulgata omnibus patent. Vale Vir Doctiss: me dum me tibi plurimum commendatum uolo.

Dabam Romæ Die 30 Martij 1693.

Doctissimo et Præclarissimo Viro Domino Matthæo
Fabio Civitatis Imperialis Heilbrunnæ Archiatro.

[*Translation.*]

Marcello Malpighi
to the very learned and renowned man
Master Matthew Faber the most excellent
professor of medicine

Chronic feebleness of my body and continual cares so occupy me that I am altogether unable to find leisure for my studies; wherefore, abandoning meditations and observations and acting as doctor to the supreme Pontiff, I am unable to be of service to my friends and to my own inclinations; hence, most learned man, I beg you to have me excused if I shall be unable to begin further researches into the structure and nature of the *pila marina*. The meditations which I formerly communicated to you are quite immature, and not worthy of publication. I have nothing concerning our own phosphorus and its legitimate preparation except those published [writings] by various authors which lie open to all. Farewell most learned man, I wish to commend myself most sincerely to you.

Given at Rome on the 30th day of March 1693.

To the most learned and renowned man Master Matthew Faber, Chief Physician of the City of Imperial Heilbronn [Würtemberg].

Johann Matthæus Faber, to whom this letter was written, was the author of 'Strychnomania . . .', Augustæ Vindel., 1677, a quarto which stated on the title-page that he was 'Heilbronnensis medicus'. In Eph. Nat. Cur. Dec. II, Ann. x, Appendix, 1692, Faber gave an account, 'Pilae marinae anatome botanologica'. (See Sir Sidney Harmer's account of *pila marina* in his Presidential Address, 24 May 1929,—Proc. 141 Sess. 1928-9, p. 75.) 'Our own phosphorus' seems to refer to the form of phosphorus found in an earth near Bologna, Malpighi's native town, and named Bolognian phosphorus.

A pencil note on the verso of the letter reads, 'Marcello Malpighi 1628-1694 ex coll. B. Dean Jan. 1919'.

Professor Donald Robertson of Cambridge has kindly made some improvements in the above text and translation.

NEHEMIAH GREW AND MARCELLO MALPIGHI.

BY AGNES ARBER.

It is impossible not to feel a certain sense of guilt when, in honour of Nehemiah Grew's tercentenary, one attempts to discuss and appraise his work, for this can be done only in defiance of his express behest. He wrote in his first book: 'how far I have gone, I neither judge my self, nor leave it to any one else to do it; because no man knows how far we have yet to go, or are capable of going. Nor is there anything which starves and stinteth the growth of knowledge more, than such Determinations'. One can only hope that after 300 years this prohibition may be held to have lapsed, and that Grew, who approved of scientific academies, may, from the shades, gaze with some benevolence upon the Linnean Society's celebration of his long-ago birth, and may even take a remotely reminiscent pleasure in the thought that his own name, and that of his great colleague, Marcello Malpighi, still meet 'and part and meet again, Where dead men meet, on lips of living men'.

We do not know the exact day of the year from which to date Grew's tercentenary. We only know that his baptismal entry in the register of St. Peter's Church, at Mancetter, near Atherstone in Warwickshire, gives, under September 1641, 'Nehemiah Grew Sonne of Mr. Obadiah Grew and Ellen his wife bap^d the six and twentieth day'. Nehemiah's father, born in 1607, was a clergyman and schoolmaster, who had studied at Balliol College, Oxford. In the Civil War, though he at first supported the Parliamentary party, he was never an extremist, and, when the Restoration came, he welcomed it. In 1662 he lost his living, through his decision not to comply with the Act of Uniformity, and he eventually founded a Presbyterian congregation. He must have been a man of

courage and pertinacity, for he made more than one effort to induce Cromwell to spare the life of Charles I. Obadiah Grew married Helen, or Ellen, the daughter of Gregory Vicars, and the widow of William Sampson, a playwright. We may conclude that she succeeded in fusing her two families harmoniously, since Nehemiah Grew is known to have received sympathy and encouragement in his botanical work from his half-brother, Henry Sampson, his senior by about a decade. He followed Henry, and his brother, William Sampson, to Pembroke Hall, Cambridge, taking his B.A. when he was twenty. After the Restoration of Charles II, Nehemiah's dissent must have prevented his pursuing a Cambridge career, and he sought the more liberal atmosphere of Leyden University, where he studied medicine, again following in the footsteps of Henry Sampson. He returned to England as an M.D., and, after a period at Coventry, he took up his abode in London, being urged to this move by the Royal Society. About his home life we know little. 'The Dictionary of National Biography' states that he was married to Elizabeth Dodson of Cheshunt, and that he had at least one son and two daughters. No other marriage seems to have been recorded, but, from Mrs. Marion E. Grew, whose husband, Mr. Edwin Sharpe Grew, can claim descent from Nehemiah, I learned of an inscription in Christ Church, Newgate Street, indicating that there had also been an earlier marriage. I asked the help of the Vicar, the Rev. T. R. Hine-Haycock, who, with difficulty, discovered the monument skied in a dark corner of the church, so that the inscription could not be read except from a ladder. He very kindly undertook to have a rubbing made of it, but on 29 December 1940, immediately after he had identified the tablet, the church was burnt out by enemy action, and it seemed probable that the inscription was lost for ever. However, in April, when a search could again be made, it was found that this was almost the only mural memorial which had survived with its lettering in a decipherable state, and that a bust, which had surmounted it, though it had been thrown several yards and mutilated, was not destroyed. Mr. Hine-Haycock was able to get a complete copy of the Latin words, which record the death, on 9 April 1685 in the twenty-seventh year of her age, of Mary (daughter and co-heiress of Richard Huetson, Merchant, and of Grizel), who married Nehemiah Grew, Doctor of Medicine. She must thus have been some eighteen years younger than her husband. The inscription, which is couched in the language of real feeling, speaks of her as distinguished by beauty of person, mind, and character. In 'Cosmologia Sacra', the theological and philosophic work to which Nehemiah Grew devoted much time in later years, we read

that ' Pillars, Statues, and other Memorials, are a sort of Shaddow of an Endless Life ; and shew, an Inextinguishable Desire, which all Men have of it '. One wonders if, when he penned these words, he had before his mind's eye the monument which he had erected long ago to his young wife.

Grew's medical career was active and successful ; it does not, however, concern us now, except as a background against which his biological research must be visualized. His scientific life centred in the Royal Society, then in its most stimulating phase of early freshness. Grew reported on his work to the Society at short intervals, and his accounts were received with cordial appreciation. To take an instance at random : on 9 November 1676 ' Dr. *Grew* read a discourse concerning flowers, accompanied with many elegant and curious schemes [i.e. diagrams] in presenting the particulars discoursed of. He had the applause of the Society, who declared the discourse and figures very well worth publishing '.

The Royal Society did not confine itself to praising and printing Grew's work ; it also took practical steps to promote his researches. At a Council Meeting on 10 April 1672, ' The bishop of Chester proposed Dr. *Grew* to be curator to the Society for the anatomy [of] plants for a year, upon subscriptions, amounting to fifty pounds, to be made by such members as should be willing to contribute thereto. The council approved of this proposal '. This must be one of the earliest instances of the definite and formal subsidization of research by a learned academy. In 1677 Grew became one of the two Secretaries of the Royal Society, his colleague being Robert Hooke. The foreign correspondence of the Secretaries must have been one of their most exacting tasks. The long and regular communications, often in Latin, which they exchanged with savants on the Continent, to a great extent took the place of the circulation of journals and offprints, which today interconnects research workers all over the world. Grew seems to have played his part fully in these exchanges.

The initiation of the Royal Society can be traced back to about 1645, when ' several worthy persons residing in London, who were inquisitive into natural, and the new and experimental philosophy, agreed to meet weekly on a certain day, to discourse upon such subjects '. Among these worthy persons was Francis Glisson (1597-1677), who was also concerned with the more formal foundation of the Society in 1660. He was a man of remarkable powers, who afterwards became Regius Professor of Physic at Cambridge ; he is remembered especially for his pioneer treatise on rickets. In a later volume, the ' *Anatomia Hepatis* ' of 1654—written, like his other books, in Latin—a passage occurs

which may be rendered freely as follows: 'Plants also come under this heading [of possible subjects for anatomical study], for they agree with animals in the varying structure and diversity of their parts; and doubtless from accurate dissection of them, extremely useful observations would accrue to us; and it would be better to devote one's energies to the examination of these objects—though they may be of a lower order—than to pass one's life uselessly, as often happens, in transcribing the labours of others'.

These words of Glisson's seem to be the first direct suggestion, since the great days of Greek botany, that the anatomy of plants might be worth pursuing as a corresponding discipline to the anatomy of animals. Nehemiah Grew tells us that in 1668, when he had already been studying plant structure for about four years, he communicated his design to his 'brother-in-law' (or, as we should now say, his half-brother), Dr. Henry Sampson, who then drew his attention to this passage in Glisson, which Grew felt to be so apposite that he set it in the forefront of his first book—'The Anatomy of Vegetables Begun', published in 1672. It is regrettable that, in modern botanical language, the word anatomy has been narrowed to signify microscopic structure exclusively. To Grew, who adopted it from human and animal anatomy, its meaning also included what we should now call general morphology. So, before considering the detailed microscopic anatomy, which is generally held to be his chief claim to remembrance, it may be well to glance very briefly at one or two points in his contribution to the broader knowledge of plant structure. This contribution was essentially dynamic. He urges those who wish to study the subject at first hand to 'begin, and so proceed till they end again, with the Seed', and not to confine 'their Enquiries to one time of the Year; but to make them in several Seasons, wherein the Parts of a *Vegetable* may be seen in their several Estates'. His visualization of the whole life-history as a dramatic sequence, imparts a certain excitement to his descriptions. After the radicle has 'shot into a Root, 'tis now time', he writes, 'for the *Plume* to rouse out of its Cloysters In order whereto 'tis now fed from the Root with laudable and sufficient aliment'. What we, by a luckless misnomer, call the 'vascular system' of the seed, he names the 'inner body'. He describes the way it branches within the cotyledon, and uses the term 'seminal root' for the brush of bundles, saying that the parenchyma is related to the 'seminal root' as the earth is related to the plant root itself. This extended use of the term 'root' is somewhat startling, but it is of course true that part of the function of the veins in the cotyledon is to draw supplies from it and pass them to the young plumule, as the roots in a pot of mould

absorb water and salts, and pass them on to the growing regions.

When Grew turns from the seedling to the construction of the mature plant, we find that he has a perfectly clear idea of the nature of buds, and the process of their development into shoots; 'the *Germen*', as he says, 'being prolonged, and so displaying its several parts, as when a *Prospective* or *Telescope* is drawn out, thus becomes a *Branch*'. He notices with interest the precocious development of leaves in the bud. The '*Buds* of all *Trees*', he writes, 'consist of a great number of *Leaves*, all perfectly formed to the Centre; where, notwithstanding, they are sometimes, not half so big as a *Cheese-Mite*. So that all the *Leaves* which stand upon a *Branch* . . . of one whole Years Growth, were actually existent in the *Bud*'. How pleased he would have been with the twentieth-century discovery (Moore, E., 1909) that, in the horse-chestnut winter-bud, not only are all the leaves for next season formed, but also the first two scales for the succeeding winter-bud. Grew observed, also, how long before their appearance the development of flowers may occur. For instance, he noticed and figured next year's flower in a tulip bulb in September, with the perianth, stamens, and gynaecium already in being. Such facts suggested to him that, since blossoms are thus in existence in the winter, they might be forced to expand in the cold season, 'by keeping the *Plants* warm, and thereby enticing the young lurking *Flowers* to come abroad'.

Important and numerous as were Grew's observations on macroscopic structure, they had not the pioneering quality of his work on microscopic anatomy, to which we must now turn. In his first book this did not play any major rôle. 'Only in some places', he writes, 'we have taken in the help of Glasses', and he goes on to explain that the microscopic part of his work was inspired by Robert Hooke. He says that after 'the whole *Composure*' had been finished, 'some observations made by that Ingenious and Learned Person, Mr. *Hook*, a Worthy Member of the *Royal Society*, my much Honoured Friend, and by him communicated to me, were super-added; As likewise some others also *Microscopical*, of my own, which his gave me the occasion of making'. The only illustrated description in '*The Anatomy of Vegetables Begun*', relating to microscopical structure, is that of the burdock stem, a small part of which is drawn in transverse section. The parenchyma is represented as definitely cellular, and three well-defined bundles are shown, one more marginal, and two nearer the centre of the stem. Grew calls the outer bundle, and also a fibrous band on the edge of the section, 'The outmost shooting of the *Lignous Body* distributed into

the Leaves'. On cutting sections of the stem of this plant for comparison with his results, I have found that his description is substantially correct; the outer strand is probably the median bundle for a leaf. The two bundles further in, which he calls 'The inner Shootings or Fibres distributed to the Branches', seem to be rightly identified; they look like two bundles for the lateral branch, which do, in fact, occur within, and on either side of the leaf trace. Grew draws the fibrous caps of the bundles, which he realizes are not merely solid masses, for he writes, 'The Black Specks are their Pores, which through a *Microscope* are fairly visible in them all'. He does not clearly distinguish the phloem, but the general form of the bundle, and the relation of the fibres to the rest of the tissues, are well seized. This figure of the burdock stem may claim pride of place as the first picture in any printed book showing vascular bundles in section. The fact that 'The Anatomy of Vegetables Begun' includes only this one microscopic drawing is not a matter of chance, for all Grew's work was done on a preconceived plan; foresight was an integral element of his mind. 'No man could draw a Picture, or compose a Tune', he says, 'if he had not every stroak of his Pencil, and every Note, drawn and sung in his Phancy beforehand'. One is reminded of a small child's description of the process of drawing: 'I think, and then I put a line round my think'. The priority which Grew gives to naked-eye observation is as intentional as any other feature of his scheme. 'I had examined the Parts', he writes, 'chiefly by the bare eye: some few Observations excepted, which were made by the Microscope. And this I did, to the intent I might make proof, both for my self and others, how far it is possible to go with the eye, without the help of Glasses: purposing afterward to make the utmost use of those also'. This purpose was fostered by the Royal Society, for on 8 May 1672, when Grew had been newly appointed Curator for the anatomy of plants, he 'was desired to produce some observations on that subject at the next meeting . . . In order to which it was ordered, that Mr. *Hooke* should deliver to him the Society's microscope'. It may be assumed from this record that Grew either possessed no microscope of his own, or an inferior one. It is evident that he at once made good use of the instrument allotted to him, for his account of roots, published in the next year, includes a number of highly elaborate microscopic drawings. In 1675 this book was succeeded by a description of stem structure called 'The Comparative Anatomy of Trunks', which was still more thoroughly illustrated with drawings of transverse sections. In 1682 he summed up his work by producing a folio called 'The Anatomy of Plants', which consists, in part,

of amplified second editions of the three small books which preceded it. In considering Grew's initiation of plant anatomy it seems more repaying to treat all his volumes together, and to try to understand his notions under subjects, rather than to analyse them chronologically.

The fact that Grew looked upon naked-eye observations as fundamental, gave his anatomy a sound and realistic basis. He is urgent 'that both immediate and microscopic Inspections be compared; since it is certain, that some things may be demonstrated by reason and the eye conjunct, without the Glass, which cannot be discovered by it'. The features of detailed structure which he himself was able to detect without a microscope are sometimes startling; he says that only 'three things' are demanded, 'viz., a good eye, a clear light, and a Razor wherewith to cut'. So armed, he succeeded in discovering even such a small-scale feature as the concentric nature of the bundles in the iris rhizome. He speaks of these bundles in the 'Flower-de-liz' as being 'visibly concave, each of them, in their several Cavities also embosoming a very small *Pith*; the sight whereof, the Root being cut traverse, and laid in a Window for a day or two to dry, may without Glasses be obtain'd'. To see exactly what the structure was, to which Grew refers, I cut sections of the rhizome of a garden iris, probably *germanica*, and found that the individual bundles were incompletely amphixylic—the xylem surrounding the phloem (which Grew calls the 'pith' of the bundle) with a break on one side. I also examined the cut surface, dried as Grew describes, and I found that with a lens it was possible to detect the concentric character, but I, personally, should never have seen it for myself in the first place with the naked eye, especially if I had looked at the rhizome, as Grew must have done, with no preconceived ideas about bundles of this kind.

It was probably the constant reference to naked-eye observation which kept Grew's work so admirably three-dimensional. He recommends the use of perpendicular, transverse, and oblique sections, but his illustrations show that his actual practice was based upon the much better plan of substituting tangential for oblique sections, a change which was possibly due to the influence of Malpighi. It is remarkable that even in this early phase of the subject, Grew had the insight to anticipate modern methods in recognizing that transverse sections are much the best source of information about the general scheme of plant anatomy. In 'The Comparative Anatomy of Trunks' (1675), he says: 'I have chosen to give my examples chiefly in the transverse Section', because the 'Size, Number, and Position' of the parts, and 'their Regularity and Constancy . . . are this way, much more

clearly and certainly represented'. The expression 'transverse section', now universal in anatomical work, seems to have originated with Grew. It is clear that he had arrived also at the idea that the vascular structure could be understood by means of *serial* sections, for, in describing the bean seedling, he says that the 'inner body' [i.e. the vascular cylinder] appears most plain and conspicuous in cutting the *Radicle* athwart, and so proceeding by degrees toward the *Plume*, through both which it runneth in a large and straight trunk'. It may be worth noting that Grew was apparently the first botanist to speak of using transmitted light for examining sections (though not with a microscope), for in order that the vessels of a root may be seen, he recommended in 1672 that 'a very thin Slice cut athwart the young Root of a Tree' should be 'held up against the light'. A little later Leeuwenhoek took a step beyond Grew, for in a letter dated 1674 he suggested that transmitted light should be used in looking at pith, etc., through a microscope.

When we turn from Grew's methods to his actual results, one of the first points to consider is the relation which his work bears to the cell theory. In 1665, seven years before Grew's first publication, Robert Hooke (1635-1703) brought out a book called 'Micrographia', in the course of which he described the anatomy of cork and charcoal. He examined, 'on a black object Plate', a thin slice cut from a smooth surface of cork, and observed that it consisted of unit structures, to which he gave the rather unfortunate name of 'cells', from their resemblance to the compartments of a honeycomb; these were not, of course, the living elements of the plant, but the dead walls of those elements. He found the same honeycomb-like texture in various piths. It was from Hooke that Grew took over the idea of cells. He came nearest to grasping the exact nature of tissues composed of these units when he was studying such parts as the root cortex, of which we may quote his description. It should be mentioned that he uses the word 'parenchyma' practically as we do now. It was he who introduced it into botany; it may have been suggested to him by Glisson's 'Anatomia Hepatis', where it is used in connexion with animal tissues. Grew says that in the root cortex the microscope reveals that the 'pores are all, in a manner, spherical, and this part nothing else but an infinite Mass of little Cells or fixed Bubbles. The sides of none of them are visibly pervious from one into another, but each is bounded within it self: So that the Parenchyma of the Bark is much the same thing, as to conformation, which the froth of Beer or Eggs is as a fluid, or a piece of fine Manchet [white wheaten bread] as a fixed body'.

At first sight it is tempting to conclude from Grew's remarks

about plant cells that he had indeed arrived at the cell theory, but this was not so. We realize that he was far from a clear idea of the cell as a primary unit when he compares the cortex to 'a most exquisitely fine-wrought Sponge'. He speaks also of certain '*parts of a Vegetable*, which are neither formed into visible *Tubes*, nor into *Bladders*'. It is probable that here he was misled by the zoological analogy to which he constantly turned, for there are many parts of animals which, on casual inspection, might easily pass for non-cellular. He not only failed to grasp the fact that the plant body was completely cellular, but he also held that he had discovered the ultimate structural units, which were not cells, but something on a much minuter scale. These units were, he thought, extremely delicate fibres (which he suggested tentatively might be themselves tubular) running from cell to cell, as well as forming the walls of the cells. We must remember that his analysis of structure referred only to cell-walls; he knew nothing of protoplasm. When one thinks over Grew's notions—even those which at first sight seem fantastic—one often finds in them some faint foreshadowing of later developments. His fibrillar theory of the cell-wall, for instance, seems not inconsistent with certain modern views regarding the intimate structure of cellulose. Grew's application of the fibre idea to the composition of tissues in general is, however, vitiated by too fixed a belief in the cogency of the medieval argument from analogy; having compared the vessels to the warp and his 'fibres' to the woof of a woven material, he became convinced that this analogy was a realistic presentation of the facts.

When the new experimental philosophy, as it was called, came into its own in the seventeenth century, it was accepted with complete and touching faith as the royal road. Observation was exalted as the one thing needful, and the part which hypothesis must always play in scientific explanation tended to drop out of sight. It is an example of this attitude that Grew's picture of the plant as formed of fibrils was not, to him, a theory, but an objective fact which he felt competent to demonstrate; indeed, he showed to the Royal Society on 22 May 1672, 'in a microscope, the conformation of the pith in vegetables, viz., that the whole pith is nothing but a . . . wonderful complication of exceedingly small fibres'. Grew's difficulty here, as elsewhere in his work, was that he was born too soon; his mind was constantly outdistancing the technique of his period. His microscope was crude; his illumination was primitive; he knew no way of using transmitted light; and no methods of preparing and staining sections were available to him. With such drawbacks, many people would have made no effort at an elaborate interpretation of what

they saw. Upon Grew's sanguine temperament these drawbacks worked, however, the other way, and when he gazed at the imperfectly defined image under his lenses, he did not always distinguish between the actual pattern on his retina and the vivid mental picture formed by his inward eye.

Discussing the negative facets of Grew's anatomy is a thankless task; one is glad to turn to his positive achievements. In attempting to understand his ideas about structure, it has to be remembered that he used the word 'fibre' not only for his hypothetical ultimate unit of plant composition, but also for the vascular bundle as a whole, and sometimes for certain of its components. He realized thoroughly, however, that the 'fibre', in the sense of a vascular bundle, was a complex structure, 'perforated by 30, 50, 100, or hundreds of Pores'. He calls the wood as a whole 'a Cluster of innumerable and most extraordinary small Vessels or concave Fibres'.

On the broader aspects of structure Grew was sometimes surprisingly clear; he had, for instance, an adequate idea of the nature of the external coats of the root. 'Every Root', he says, 'hath successively two kind of skins: the one coetaneous with the other parts; and hath its original from that which involveth the parts of the Seed it self [i.e. the epidermis]. The other post-nate, succeeding in the room of the former as the Root ageth; and is originated from the Bark'. Here Grew indicates, if somewhat confusedly, the existence of the pericyclic corky layers which so commonly occur in the root, and outside which the tissues exfoliate. He recognizes that the shelling off of these tissues may leave the xylem close to the root surface, 'the very Vessels themselves, in many Roots [thus] coming under an apparent view, and standing in the utmost surface of the Root'.

The growth of stems in thickness naturally engaged Grew's attention, and he reached a sound general conception of the secondary development of wood, though he could not detect the details with the means at his disposal, nor did he realize that there was an increase in the phloem as well as the xylem.

It was not only root and stem anatomy which interested Grew; he also examined leaf-structure, and arrived at a distinct notion of its essential dorsiventrality. He observed that the bundles of the leaf-base and petiole are not 'in an even Line; but alwayes in either an Angular or Circular posture, and usually making either a Triangle, or a Semi-Circle, or Cord of a Circle . . . The usual number of these Nerves or Fibres is 3, 5, or 7'.

In addition to vegetative anatomy, Grew also studied the structure of fruits; he gives a noteworthy account of the vascular system of the apple. In 'The Anatomy of Vegetables Begun' he writes: 'The main Branches are usually fifteen;

ten are spread and distributed through the *Parenchyma* . . . the other five . . . are originated from one . . . running along the Center of the *Stalk* . . . To these the Coats of the *Kernels* are fastened'. Grew thus evidently distinguished the 10 bundles of the perianth-stamen system, as well as the ventral bundles of the carpels. The latter usually take the form of five pairs belonging to adjacent carpels, rather than the five single bundles which he describes. In the most recent anatomical account of the apple fruit (MacArthur, M., and Wetmore, R. H., 1939) it is striking to find Grew's work cited in the list of references, which is otherwise entirely of the twentieth century. In this paper it is shown that the members of the ventral bundle pairs may fuse, so that Grew may have been right when he reported the existence in his material of five bundles only, associated with the attachment of the seeds. In the second edition of his description (1682) it is improved by the record that the carpels also had five dorsal bundles; these median strands had formerly escaped his eye.

It is a surprising and saddening fact that, after Grew, plant anatomy remained almost at a standstill right into the nineteenth century. That the subject should have marked time for so long may be due in part to the fact that Grew was not one of a line of teachers, so that he had no opportunity of educating younger men to carry on the work from the point at which he left it; but though he had neither master nor disciple, he had one great confrère, and to him we must now turn.

Marcello Malpighi was born at Crevalcuore, near Bologna, on 10 March 1628; he was thus thirteen years older than Nehemiah Grew. He relates, in the fragmentary autobiography which is included in his 'Opera Posthuma', that, in 1645, when he was seventeen or eighteen, his grammatical training being completed, he turned to philosophy, and eventually to medicine. After taking his doctorate in both disciplines, he held teaching posts at Bologna and then at Pisa. He speaks of the close and fruitful intercourse he enjoyed at Pisa with many savants, including Borelli, who made his mark by his application of mathematical ideas to living things. Malpighi's life at Pisa must have been as intellectually inspiring as Grew's life in London, in the days when he was in constant contact with other Fellows of the Royal Society. Unluckily, Malpighi, who was a very delicate man, was compelled to leave Pisa and return to Bologna after three years, for reasons of health. In 1662, however, he was made professor at Messina, where he remained for four years. Then, after a further period of more than twenty years at Bologna, he became body physician to Pope Innocent

XII, an appointment which took him to Rome, where he died on 29 November 1694, aged sixty-seven. Grew, who lived until 1712, thus survived Malpighi for many years, but the botanical work of the two men was all published between 1672 and 1697, that is to say, roughly, in the last quarter of the seventeenth century.

Malpighi became famous for his work on human and animal anatomy, with special reference to embryology. His botany may be considered a secondary activity, but it is this alone with which we are here concerned. Like Grew, he was intimately associated with the Royal Society, which, even in its seventeenth-century infancy, was strongly international in character. Although Malpighi carried out all his work in Italy, and never visited England, the Royal Society sponsored his researches, side by side with those of Grew, with complete impartiality, and published the writings of both men in the form of splendidly illustrated folios. Most regrettably, Schleiden, towards the middle of the nineteenth century, made serious allegations against Grew of bad faith toward Malpighi, and of plagiarism from his writings; Grew's reputation still suffers to some extent from these accusations. I have analysed the relation of the two men elsewhere (Arber, 1941 *b*), so I will only say here that Schleiden's statement is demonstrably a tissue of errors as regards dates and facts, and that, after working over the matter in detail, I have come to the conclusion that Grew emerges without a stain on his character, and that he shows nothing throughout but friendliness and admiration for Malpighi, unsullied by any hint of jealousy.

The reasons which led Malpighi to approach the interpretation of plants, or, as he calls them, 'this lowest order of creatures', are set forth in the beginning of his first botanical book. They may be translated as follows: 'In the enthusiasm of youth I took to anatomy, and although I was uneasy about certain points, I sought, nevertheless, to investigate it in the higher animals [in perfectionibus]. But since these matters are involved in their own special difficulties and are exceedingly obscure, they call for a comparison with simpler cases. From this point of view, the idea of the examination of insects at once made an appeal to me. Since, however, this also has its own difficulties, I next turned my mind to the investigation of plants, in order, after long study of the plant world—returning in my course by the stair of *Natura Vegetans*—to open the way again to my earlier studies. But perchance even this will not suffice, since the simpler world of minerals and of the elements ought to be dealt with first'.

In the work to which Malpighi was led by these considerations, he reached, like Grew, some notion of cellular structure, with 'little bladders' (utriculi) as the basic units. He speaks

of the cortical elements as utricles which are turgid with transparent sap. Of Malpighi's histological discoveries, the one which struck Grew as the most important, and for which he expresses special indebtedness, is that of spiral tracheids or vessels. Malpighi also illustrated a number of other detailed features, such as tyloses in vessels, and pits in the tracheids of *Abies*.

The argument from analogy, which was constantly present in the minds of biologists of the pre-modern period, was invoked by Malpighi, as often as by Grew, in order to throw light upon the construction of plant tissues. Both men, when they began to realize that plants were formed of more or less spherical cells, intermixed with elongated vessels, were puzzled as to how these individually bubble-like and tubular units held together to form anything so firm and solid as the trunk of a tree. They do not, in fact, speak of this difficulty explicitly, but I think it may be deduced from their attempts to explain plant structure. For example, Malpighi represents the medullary rays and the bundles, in a radial section of *Prunus* sp., as interlocking like interlacing basket-work; as we have already noted, this sort of analogy was one to which Grew continually reverted.

Malpighi's work on external morphology is quite as remarkable as his anatomy. It is illuminated throughout by his controlling interest in embryology and development. It deserves prolonged study, but we cannot do more here than mention its existence.

Having touched upon the initiation of plant anatomy at the hands of Grew and Malpighi, we must in justice turn for a moment to the Dutchman, Antony van Leeuwenhoek, whom we have already named incidentally. In age he came between Malpighi and Grew. He was not primarily a botanist, but rather the forerunner of those biologists who are now called protozoologists and bacteriologists. He was, nevertheless, interested in Grew's work, and he took trouble to try to criticize it. For instance, in 1676 he wrote to the Royal Society that he had seen Grew's 'Comparative Anatomy of Trunks', but, by reason of his 'unskilfulness in the English Tongue', he 'could have little more than the contentment of viewing the elegant cuts'. He sent some comments, with a rather good drawing of a transverse section of an ash twig of a year's growth. A pitted vessel is also shown in detail—it is perhaps the first ever figured—though Leeuwenhoek misunderstood what he saw, and thought that the vessel was full of 'globuls'. He did not attempt systematic studies in plant anatomy at all comparable with those of Malpighi and Grew, so this slight mention of his work may perhaps suffice.

After this brief glance at the anatomical studies of Grew's

contemporaries, we must return to him himself, and consider certain broader aspects of his scientific thought*. His standpoint was basically religious, and he felt it his duty to adjust the more objective view of the universe so that it should not conflict with the anthropocentric ideas then inculcated by the churches. In this he may have owed something to Descartes, who also made a definite effort at such a compromise. Descartes wrote, 'that God has created all things for us . . . is in some respects true, because there is nothing created from which we cannot derive some use, . . . it is yet not at all probable that all things have been created for us in such a manner that God has had no other end in creating them'. Grew developed this idea, and believed that a structure might be held to have more than one purpose, according to the point of view from which it was regarded. For instance, in treating of roots, he notes that if the cortex is bulky, as in chicory, asparagus, etc., it is 'therefore taken for the prime Part; which, though, as to medicinal use it is; yet, as to the private use of the Plant, not so'. In his discussion of the androecium, Grew made considerable play with similar notions. At first he was much puzzled by the 'attire' (stamens), which he analysed into 'chives' (filaments) and 'semets' (anthers). He considered that the attire might exist for the sake of the pleasure given to man by its ornamental qualities, but he was not quite satisfied about this, for he thought that the anthers would be even more beautiful if they did not break open, so the existence of the pollen could not be explained on the pleasure-to-man hypothesis. 'Distinction'—or, in other words, the possession of recognizable features—was another quality in plants which might be accounted for by its usefulness to man, but Grew was not quite satisfied about this either, since, though the attire might serve for differentiating plants when a magnifying glass was used, he did not think it helped much in the passing view it generally received. He realized, however, that the attire might serve for food and for distinction to other animals, 'that they may be able to know one Plant from another, and in their flight or progress settle where they like best', and that it might thus conform to the purpose of 'the Great Master', who 'some where or other carveth out to all', and 'for a great number of these little Folk, . . . hath stored up their peculiar provisions in the *Attires of Flowers*'. Having gone through all these considerations, Grew confessed with characteristic honesty that he knew he had not even then got to the bottom of the matter, and that the plant's own point of view, which eluded him, was after all the main thing;

* On Grew's mechanistic theory of the universe, see Arber (1941 a).

so he concluded, 'lastly, what may be the primary and private use of the *attire* (for even this above said, though great, yet is but secondary) I now determine not'. These words occur in 'The Anatomy of Vegetables Begun' of 1672, but in 1682, when his lecture on flowers, read before the Royal Society in 1676, was first printed, he went further, and solved the problem in general, if not in detail. He says that in discourse with 'Sir Thomas Millington, he told me, he conceived, That the *Attire* doth serve, as the *Male*, for the *Generation* of the *Seed*'. It was unselfish of Grew to give the credit for this suggestion to Millington, for he must have arrived at it himself independently, since he tells us, 'I immediately reply'd, That I was of the same Opinion; and gave him some reasons for it, and answered some *Objections*, which might oppose them'. Sir Thomas Millington (1628-1704) was a medical man, born in the same year as Malpighi. Grew made the slip of calling him 'Savilian' Professor; actually he was Sedleian Professor of Natural Philosophy at Oxford. It is difficult not to feel a certain doubt as to whether his remark about the stamens was more than a happy shot in the dark, for another passage, in which Grew mentions him, shakes one's faith in him as a naturalist. Grew's words are: 'And though I have not seen it my self, yet I have been told by one that doth not use to phancy things, that the Volatile Salt of *Vipers*, will figure it self into the semblance of little *Vipers*'; and a note is appended naming Sir Thomas Millington as the observer who did 'not use to phancy things'. Perhaps one ought not to be prejudiced against Millington for thinking he saw what he expected to see, for a belief that salts derived from a plant or animal represented, as it were, its essence, and displayed its characteristics, was widely held at that period. Grew accepted this belief unquestioningly. In a frost, 'The Dew upon Windows', he says, 'or water upon flat, smooth, and broad Stones, will sometimes be elegantly flourished into a Vegetable Form. The Congealing Principle being assisted herein by the *Volatile Parts* of Plants, which continually perspire, and hover in the Lower Region of the Air in greater Plenty'. Grew makes ingenious application of the idea of this free and ghost-like existence of plant essences, to account for plant fossils, or stones with markings recalling vegetable growths. He thought that the 'Salts of Plants, . . . washed down with Rains, and lodged under ground', might be 'disposed into such-like figures'. Absurd as these notions seem to us now, it must be recognized that the men who held them were groping, if dimly, after the modern conception that, in a certain aspect, it is the chemical constitution of the plant which finds expression in its form.

It was one of Grew's great merits that he always tried to

treat structure and function concurrently. His results, however, were not so good as his aim, since he relied on deducing physiological laws from structural observations, and, moreover, he was always hampered by the primitive state of chemistry and physics at that period. Yet, as in everything he touched, he made a certain number of illuminating suggestions. He foresaw, for instance, that organic compounds might come to be made synthetically in the laboratory, and he also faintly foreshadowed the continued independence of the parental contributions in fertilization.

In histories of science Grew is liable to be docketed simply as a pioneer in plant anatomy, but the width of his purview outside this field is astonishing. In one of his chemical works he remarks, 'The *Experiments* may seem too numerous . . . But no less a number would have answered the design of an *Universal Survey* ; which, though less pleasing, proves more instructive in the end : not being like angling with a single Hook, but like casting a Net against a shole ; with assurance of drawing up something '. This simile forms a just summary of Grew's general method, and it may be added that he had the flair that made his net often come up with treasures in it.

Grew's biological interests were by no means confined to botany ; in zoology he also carried out pioneering studies. He made a comparative survey of the alimentary canal in a large number of animals, and he also did considerable descriptive work. This was incorporated in a catalogue of the specimens in a Museum which the Royal Society possessed at that time ; this enumeration, issued in 1681, was not the slight document which one might expect, but a solid illustrated folio. In his account of the animal specimens, he offers detailed descriptions of certain species of which he finds no exact diagnoses in previous books. He also anticipates modern methods by giving an elaborate key for the identification of shells, while in his 'Anatomy of Plants', published in the succeeding year, he makes some very good suggestions for a corresponding key for plants. In the catalogue he also discusses fossils, and, though he did not, as we have already mentioned, really understand them, he yet rejected the more fantastic current views of their nature. In his own words : 'although Nature cannot be said to imitate Art : yet it may fall out, that the effects of both may have some likeness', and he instances certain objects, which were doubtless fossil foraminifera, which he describes as 'Those white Concrections, . . . *Confetti de Tibuli* . . . sometimes so like round *Confects*, and the rough kind of *Sugar'd-Almonds*, that by the eye they cannot be distinguish'd'. He adds, however, 'To call these *Petrify'd Sugar-Plums*, were senseless'.

The cabinets of curiosities of the seventeenth and eighteenth

centuries—the original stocks from which the highly specialized museums of today have been evolved—were as synthetic as one expects ancestral stocks to be. That of the Royal Society contained miscellaneous objects of every kind. Grew had to catalogue not only scientific specimens of serious value, but also knick-knacks, such as ‘A Little *Box* Turn’d out of a *Nutshell*’; or, ‘A Natural *Landskip*, or Prospect of Ruinous Buildings in Stone. Humour’d with a *Tree* painted over it; or, a *Carved Shell* of *Mother of Pearl*’, showing Andromeda and the Monster, with Perseus on Pegasus flying to the rescue, ‘done’, as Grew remarks, ‘with extraordinary Art’. Having to spend time on bibelots of this kind does not seem to have gone against the grain with him; indeed, his books often reveal evidence of his keen awareness of visual impressions, and of his vivid response to artistic quality. This was one of the factors which gave his style a certain glowing tone, rare in scientific writing. He was unusually word-conscious; he complains, for instance, of what he calls ‘the penury of *Language*’, when he is trying to describe the variety of tastes among herbs. That he thought much about modes of expression is evidenced by a copy of ‘The Comparative Anatomy of Trunks’ (1675), preserved at the British Museum, which is emended with extreme fullness and elaboration. Much of the correction is incorporated into the second edition of 1682, but by no means all. It appears that yet another corrected copy, to which he refers as ‘ye Book Interleavd’, must have preceded the 1682 version. The corrections include many amendments in the use of capitals, which Grew was in the habit of employing very freely; that he took so much trouble to alter them, shows that he thought their distribution important, but I have not been able to understand upon what principle he worked in scattering them over the page. But whether we grasp the significance of his minor corrections or not, the fact remains that he cared enough about the details of expression to take untold pains to get them as he thought they ought to be. The specialty of Grew’s style, however, comes from something much more individual than laborious polishing. That its quality was partly a matter of ear, is suggested by his analytical account of the musical value he recognized in words and their groupings. ‘For in all good Speech’, he says, ‘there is a sort of Musick; with respect to its Measure, Time, and Tune. Every well-measured Sentence is proportional Three ways; In all its Parts, To other Sentences, And to what it is intended to express. And all Words, have that Time allow’d to their Syllables, as is suitable to the Letters whereof they consist, and to the Order wherein they stand in a Sentence. Nor are the words without their Tones or Notes, even in Common Talk: which together compose that Tune, which is proper

to every Sentence : and may be prick'd down, as well as any Musical Tune'. It was a piece of good fortune that Grew was born in due time to enter into the magnificent English of the seventeenth century as into a natural heritage. The authorized version of the Bible, then a modern book, no doubt set its stamp upon his language as it did on that of other men of his period. He speaks, as a naturalist, with special admiration of the 104th Psalm, and he declares that there is 'no where a Match' for the latter part of the book of Job, 'where God himself speaketh, and reads a most methodick and Noble Lecture of Natural History'. It is difficult to say how much Grew owed to other specific influences, but Sir Thomas Browne, whose writings were all published within his lifetime, and to whom he alludes, is repeatedly recalled in his turns of thought as well as his turns of speech. Indeed, there are scattered passages throughout Grew's writings which would not have been out of place in Browne's '*Religio Medici*'. Here is one such passage : 'How Dogmatical soever my Assertions may seem to be, yet do I not affect the unreasonable Tyranny of obtruding upon the Faith of any. He that speaketh Reason, may be rather satisfied, in being understood, than believed'. And here is another, which seems to have even more of the ring of Browne's voice : 'I make my own thoughts no mans Measure . . . Let them go and take their fortune without a *Flambeau* ; which being prefixed to things of so glimmering a shew, would not serve to blazon, but extinguish them'. Though the resemblance to Browne is indubitable, this may well point to a natural kinship of mind rather than to derivative ideas or phrasing, for Grew in his style is emphatically himself, and that self was essentially independent. The vivid and racy character of his botanical descriptions strikes one as being entirely his own, and as arising out of the liveliest sense of what has been called the thinginess of things. He often lights up some simple account with an unexpected metaphor, as when he speaks of plums as having, as it were, only a '*Coat of Kid*', while grape skin is 'a good thick *Buff*'; or when he describes the seed-case of the radish, in which 'the *Parenchyma* gradually dries, breaks, and shrinks up into several soft *Membranes*, in which the *Seeds*, in the centre of the *Case*, lie swaddled, as in so many fine *Calico Clouts*'.

These considerations about Grew's manner and style may appear at first glance to be irrelevant to his biological work, but I do not think that they are, in actual fact, a side issue. It was the core of originality in the man that gave his writing its peculiar verve, and that also freed his mind to anticipate, over and over again, developments which did not fully materialize until two centuries later. These hints—thrown off unselfconsciously in any and every direction—generally

fell on stony ground, for they went too far beyond the science of those days to be useful in promoting research there and then. Some of these anticipations have already been mentioned, but in conclusion it may be worth while to touch upon a few others. Outside as well as inside the botanical field, Grew showed the spirit of prophecy. He suggested, for instance, that land-bridges once connected tracts which are now separate countries, or even continents—a notion which some modern geologists have used freely. He also deserves remembrance for the idea that '*Stones*, or other *Subterranean Bodies*' ought to be treated with oil of vitriol, etc., to see if they effervesce, or produce, as he calls it, 'bullition and huff'. He thus forecasts the acid bottle, which was so familiar an adjunct of field geology in the nineteenth century.

In botany itself, one of the truths which Grew realized far in advance of his fellows was that leaf vernation was an integral part of ontogeny: 'The Formations and Fouldings of Leaves have one Date, or are the contemporary works of Nature; each Leaf obtaining its distinct shape, and proper posture together'. Troll, who stressed the same notion as recently as 1938, attributes its first formulation to Hofmeister, but Grew had made it his own long before. In connection with leaf morphology, we may also recall that Grew came very near to Casimir de Candolle's nineteenth-century discovery that peltation of the lamina was correlated with the existence of a complete vascular ring in the petiole. Grew had never happened to examine a leaf-stalk with a complete ring—so far as he had observed, the bundles never formed more than a segment of a circle—but he says that, if a complete 'Lignous Ring' were formed, it would 'shoot forth on every side, as it doth in the *Root* or *Trunk*'. We now know that this is what in fact occurs in peltate leaves.

On the question of relationship among plants, considered in its broadest aspect, we find that Grew is precisely in line with the thought of the present day. He writes that 'the most *Philosophick* way of distinguishing or sorting of *Plants*, were by the *Characteristic Properties* in all *Parts*'. It is significant that, even in Grew's tercentenary year, two modern systematists—Gilmour and Turrill—have thought it necessary to re-assert the same principle. They write: 'a taxonomist must surely take into consideration, as far as possible, *all* the attributes of living things, when making his classification'. Grew's own work did not lie in the direction of systematics, but nevertheless he had the insight to recognize that some related plants possessed related medicinal properties—in other words, a related chemistry—and to surmise that this might be a general rule. It was not until the beginning of the nineteenth century that this idea received really full expression at the hands of A. P. de Candolle.

Grew shows his intuition as much in the questions which he raises and cannot answer as in the results he actually attains. He foreshadows the holistic standpoint when he enquires, as plants pass through the 'several seasons of their lives, in what manner their convenient feeding, housing, cloathing, or protection otherwise, is contrived; wherein in this kind and harmonious oeconomy, one part may be officious to another for the preservation of the health and life of the whole'.

The intellectual renaissance was slow in penetrating to Northern Europe, and it was not until the late sixteenth, or even the seventeenth, century that it reached its full tide. Marcello Malpighi, Antony van Leeuwenhoek, and Nehemiah Grew have this in common, that they all illustrate, although belatedly, the searchlight quality of the renaissance mind which gave such brilliant but brief illumination to realms which again lapsed into darkness, and were not actually explored until after the passage of centuries. Grew's lamp, indeed—almost without his knowing what was happening—sent its rays darting over a succession of possible fields for research, some of which still await cultivation by generations later than our own. In his own words: 'For every Truth being productive: there is no Truth which can be despicable. Many a Peasant has been Ancestor to a Prince . . . the first Spectacle-maker' knew not 'that he was leading the way, to the Discovery of new Planets. Nor the first Observer of the Loadstone, that he was finding the way into a new World'.

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Discussion.—

The PRESIDENT congratulated Mrs. Arber on the vivid and interesting way in which she had described the life and work of these two great pioneers. He had always been a great admirer of Mrs. Arber's work on the history of biology and the philosophical aspects of plant morphology.

Professor T. G. B. OSBORN commented on the difficulties these pioneers must have met arising from the undeveloped state of the microscope.

Dr. J. RAMSBOTTOM asked if there was any published work of Millington's on the nature of stamens.

Mrs. ARBER replied that she was not aware of any publication by Millington on Botany.

PROCEEDINGS OF THE ANNIVERSARY MEETING

24 May 1941

Dr. E. S. RUSSELL, O.B.E., M.A., President,
in the Chair

The Proceedings of the General Meeting, held on Thursday, 15 May 1941, were read and confirmed.

The President reported the deaths of the following Fellows,—
Mr. R. Lloyd Griffiths, Mr. H. B. Lacey, Mr. J. G. Dalglish,
Sir Albert C. Seward and Mr. G. C. Turner.

The following Fellows signed the Obligation in the Book of the Charter and Bye-Laws and were admitted :—Captain Richard Charles L'Estrange Burges and Angus d'Albini Bellairs.

Certificates of recommendation of the following candidates for Fellowship were read :—For the second time, in favour of Gerald William Thomas Hunter Fleming and Edgar Wolston Bertram Handsley Milne-Redhead ; for the first time, in favour of the Rev. Alan Richard Tippet and Francis Downes Ommanney.

In the unavoidable absence of the Treasurer, his Financial Report was read by the Assistant Secretary and the Accounts of the Society, duly audited, for the year 1940-41 were laid before the meeting.

On a motion by Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., seconded by Dr. B. BARNES, the Report and Statement of Accounts were adopted.

The President announced that a Ballot for the following new Bye-Law (which was read for the third time) would be taken at the same time as the Ballot for Council and Officers,—

Add to Chapter II the following Section :—

VII. During a period of National Emergency the Council may at its discretion remit in whole or in part the Annual Contribution of any Fellow serving in the Armed Forces of the Crown or in other forms of War Service. The decision of the Council as to what constitutes War Service shall be final. The Fellow whose Annual Contribution is remitted under this Bye-Law shall not be entitled to receive the Publications of the Society during the period of remission.

The Bye-Laws regulating the Election of Council and Officers having been read by the Assistant Secretary, the PRESIDENT declared the Ballot for Council and Officers to be open, and voting began. The Ballot for Council was closed at 5.30 p.m. and for Officers at 6.0 p.m.

Meanwhile the Librarian and Assistant Secretary presented his Report.

LIST OF THE SOCIETY.—Since the last Anniversary Meeting the Society has lost 36 members. The detailed statement is as follows,—

15 FELLOWS BY DEATH.—Eustace Rolfe Gunther, Rowland Edgar Nicholas, Rudolph Beer, Joseph Burt Davy, His Grace the Duke of Bedford, K.G., Emma Louisa Turner, James Drummond, Edwin Ashby, Thomas Bates Blow, Richard Lloyd Griffiths, Henry Baker Lacey, John Gordon Dalgliesh, Sir Albert Charles Seward, George Creswell Turner, Francis Druce.

21 FELLOWS BY WITHDRAWAL.—S. M. Ahmeduddin, Robert Bernard Benson, Herbert William Pugsley, Archibald Henry Malpas, Frederick Albert Mitchell-Hedges, Richard Frederic Nevill Aldrich-Blake, Harold Augustus Hyde, Brian Seymour Vesey-FitzGerald, Francis Ralph Tubbs, Arthur Lionel Goodday, Herbert Wesley Lawton, Randolph Gordon Ridling, Lalit Prasad Khanna, Idris Giles Lewis, Lucy J. Howland Noel James Gillies Smith, William Rae Sherriffs, Harold Henry King, Walter Lowry Waterhouse, Thomas George Hill, Rubugunde Madhava Row.

In addition, 15 other Fellows have tendered withdrawals which for the present the Council has delayed acceptance.

During the Session 9 Fellows and 1 Associate have been elected. Of the 9 Fellows elected, 6 have qualified.

The present number in the List of Fellows is 646, with 3 Fellows elected but not yet qualified.

LIBRARY.—Between 1 May 1940 and 30 April 1941 6 books have been purchased and 26 books, 325 parts of periodical publications, and 16 reprints have been presented. During the same period the number of volumes bound was 250. The number of volumes borrowed by Fellows and Associates was 317 and by the National Central Library 86. 145 signatures were recorded in the Library Visitors' book.

About 3,000 volumes, picked for their rarity or association value, have been deposited in a safe place away from London; and the miscellaneous manuscripts, together with the Society's records, are being taken care of by a country Fellow of the Society of Antiquaries.

LINNAEAN COLLECTIONS.—During the Session the cases containing the Linnaean Collections have been inspected, and were found to be in good condition.

At the conclusion of this report the PRESIDENT appointed Dr. S. E. CHANDLER, O.B.E., Dr. J. HUTCHINSON and Miss M. WHITING as Scrutineers of the Ballot.

In handing the Linnean Gold Medal to Professor ARTHUR GEORGE TANSLEY, F.R.S., the PRESIDENT addressed him as follows :—

Professor TANSLEY,—Those whose pleasure lies in giving this medal to you, in recognition of your leadership in botany and your stimulating teaching, would be gratified if on the one hand it conveys to you their appreciation of your investigations in the anatomy of ferns and on the other their admiration of your great work in ecology.

You made a bridge across the gap between the old morphological teaching and the newer, more living outlook upon plants. You have been most generous and unsparing of yourself in helping others, an untiring friend to the maturing generation of British botanists. You founded, and for thirty years edited, the 'New Phytologist' as an outlet for their work—in your own words, 'throwing it on the world' to prove its survival value, and seeing your adventure abundantly justified.

You were one of those who founded the Ecological Society, and from 1916, for twenty-one years, you edited the journal of the young Society as a labour of love. In 1911 you were *primus inter pares* in the preparation of their guide book, entitled 'Types of British Vegetation', and now we are in debt to you for the stimulus of your mature and monumental work 'The British Islands and their Vegetation'.

It is in the hope that you will bring to completion, in spite of all the trouble in the world, the new British Flora on which you have embarked that, with the good will and good wishes of the Linnean Society, I hand to you this medal.

Professor TANSLEY, in accepting the medal, said he was deeply sensitive of the honour and particularly pleased that what he had done in Ecology had received this recognition.

The PRESIDENT then reviewed the welfare of the Society, as follows :—

On the occasion of this Anniversary Meeting I desire first of all to express to you my great appreciation of the signal honour you have done me in electing me as your President. I wish also to thank the Officers and Staff of the Society, who have given me unstinted help during the past year.

This has been a difficult year in the history of the Society. In contrast to the previous Session, which passed quietly, and justified my predecessor's decision to carry on normally, the beginning of the present Session found us in the midst of serious and persistent air attacks on London. In the circumstances, your Officers deemed it prudent to suspend General Meetings and meetings of Council for some months, not so much on account of the possible danger, but because of the difficulties of travel, caused by the black-out and the frequent dislocation of traffic. A Special General Meeting was, however, held on 7 November to elect a new Treasurer, and ordinary meetings were resumed on 6 March, with the intention of continuing them monthly until July.

Certain steps have been taken to safeguard the Society's property. On the advice of the Ministry of Works and Buildings, special screens were installed inside the windows on the first floor, and these proved of some value, when our windows were shattered by blast on 15 April, in protecting the Library from damage by flying glass.

The Linnaean Collections remain in a place of relative safety in the country; the Smithian and other collections have also been sent away, and some 3,000 of the most valuable books in the Library have been transferred to Oxford. In choosing which books should be removed, the Officers have received most valuable help from expert Fellows and friends of the Society, who looked through the Catalogue and indicated what books in their opinion should be selected. I desire to record the thanks of the Society to the following gentlemen for their services in this connection:—Mr. W. T. Stearn, a Fellow, Dr. C. D. Sherborn and Mr. J. Ardagh, Associates, and Mr. E. Nemes, of the staff of the Royal Botanic Gardens, Kew. We are also greatly indebted to Mr. Warren R. Dawson, who, though not a Fellow of the Society, has most generously provided accommodation for the Society's records in his country house.

Considering our central position, we have so far been fortunate in escaping serious damage. Incendiarries have fallen on or near the building on several occasions, but these have been effectively dealt with by the staff of firemen and fire watchers maintained by the Societies that have quarters in Burlington House. We are advised that the joint arrangements for fire watching are reasonably adequate, but the matter is kept under constant review. Our Housekeeper, Mr. Brown, has borne his full share in this dangerous work, and deserves great credit for his devotion to duty.

The Council have decided to take advantage of the War Damage Act, 1941, to insure against war risks the valuable Library and other effects which remain in the Rooms of the

Society, and insurance has been effected for a substantial sum. The cost will be heavy, but I am sure you will agree that this expenditure is justified and necessary.

In view of the increased cost of living, and following the precedent set by the Government, the Council have granted modest War Bonuses to the staff. Salary scales will come up for revision after the war, when the reorganization of the Library will also have to be taken in hand.

We have, unfortunately, lost a large number of Fellows through death and withdrawal. A specially grievous loss to the Society is Mr. Francis Druce, who was killed in his house by a bomb on 15 April. He was our Treasurer from 1931 to 1940, and a most admirable one. He was a generous friend to the Society, and we shall greatly miss his wise counsel.

The conditions of war have thrown an extra burden upon the Officers who have had to take upon themselves, from time to time, responsibilities belonging more properly to the Council. I wish to express my own personal indebtedness and warm thanks especially to the Botanical and Zoological Secretaries and to my predecessor in office, Dr. Ramsbottom, for the generous support and assistance they have given me.

The war has had an adverse effect upon our output of publications, which at the end of the financial year was about 45 per cent. of normal. Two further parts of the Proceedings have, however, been distributed during the last week, and these will raise the percentage to 75. This reduced output is due, not to lack of material or funds, but to the difficulties encountered by the printers, which have caused much delay in delivery. The Botanical Secretary in particular has given much time and thought to these printing problems and has sought to reduce the time-lag of our publications. Paper rationing has also to be taken into account, and the Council's policy of assigning as much as possible to the Proceedings, the paper of which is lighter, rather than to the Journal, goes some way towards meeting the Government's requirements in the matter of economy.

Let me end this short review of the Society's affairs on a more cheerful note by giving you a piece of good news. You are aware that the Council, largely at the instigation of Dr. Ramsbottom, has been looking into ways and means of making a photographic record of all the most important items in the Linnaean Collections. The botanical and zoological specimens, the manuscripts and annotated books, are, of course, priceless and irreplaceable, and though they have been removed to a place of comparative safety, it is clearly most desirable to have photographic copies made, on as large a scale as possible, and distributed to various centres of learning abroad. Careful enquiry into probable costs soon showed that

the undertaking was one far beyond our means, and it was then decided to make an appeal to the Carnegie Corporation of the United States of America for the necessary funds. This appeal has been successful, and the Corporation has most generously made us a grant of £2,000, which will enable the undertaking to be carried through on a considerable scale. We are most grateful to our American friends for this munificent gift, and see in it another proof of their practical sympathy and support for the British cause in the struggle for freedom.

We also gratefully acknowledge a contribution of £100 from the Rockefeller Foundation, through the Royal Society, towards the cost of publications.

As to the future, we shall face what is to come with fortitude, and determination to carry on, whatever difficulties may confront us. The times are hard for all of us, but I appeal to the Fellows to support the Society to the utmost of their power, so that when peace comes we may be ready to go ahead and prosper.

The PRESIDENT then delivered his Address, 'Biological Adaptedness and Specialization of Instinctive Behaviour'. [Printed in full, p. 250.]

On its conclusion, Mr. H. N. RIDLEY, C.M.G., F.R.S., moved 'That the President be thanked for his excellent Address, and that he be requested to allow it to be printed and circulated amongst the Fellows'. The motion was seconded by Dr. JOHN RAMSBOTTOM, O.B.E., and being put to the meeting was carried with acclamation.

The Scrutineers of the Ballot, who had retired at the appointed times with the voting-lists for the election of the Council and of the Officers, having completed their scrutiny, reported to the President, and he declared the result as follows :—

COUNCIL FOR 1941-42.—Dr. B. Barnes, Prof. T. F. Brooks, F.R.S., Mr. I. Henry Burkill, Mr. R. H. Burne, F.R.S., Mr. J. E. Dandy, Dr. E. Marion Delf, Mr. A. C. Gardiner, Mr. J. S. L. Gilmour, Prof. T. M. Harris, Dr. Anna B. Hastings, Mr. H. R. Hewer, Prof. T. G. B. Osborn, Mr. J. R. Norman, Dr. C. F. A. Pantin, F.R.S., Mr. H. W. Parker, Dr. J. Ramsbottom, O.B.E., Mr. Douglas M. Reid, Dr. E. S. Russell, O.B.E., Dr. Malcolm A. Smith and Major F. C. Stern, O.B.E., M.C.

(The retiring Councillors were Prof. W. A. F. Balfour-Browne, Miss M. L. Green, Dr. H. S. Holden and Mr. Fred Howarth. These, with the late Mr. Francis Druce, make five, as the Charter requires.)

OFFICERS FOR 1941-42.—*President*: Dr. E. S. RUSSELL, O.B.E.; *Treasurer*: Major F. C. Stern, O.B.E., M.C.; *Botanical Secretary*: Mr. I. Henry Burkill; *Zoological Secretary*: Dr. Malcolm A. Smith.

The President also declared that the new Bye-Law, Chap. II, Sect. VII, had been passed at the ballot held during the meeting.

The President then announced that he appointed the following as the Vice-Presidents for 1941-42:—Dr. E. MARION DELF, Dr. ANNA B. HASTINGS, Dr. JOHN RAMSBOTTOM, O.B.E., and Major F. C. STERN, O.B.E., M.C.

TREASURER'S ACCOUNTS FOR THE

(Presented at the Anniversary

Receipts and Payments of the Linnean Society

	RECEIPTS	£	s.	d.	General
		£	s.	d.	£ s. d.
To Balance at 30 April 1940:—					
Current Account at Bank		69	2	7	
Deposit Account Post Office Savings Bank		628	15	3	
Deposit Account Post Office Savings Bank (Herbert Spencer Fund)....		271	4	9	
Cash in hand		6	4	10	
					975 7 5
„ Admission Fees					12 0 0
„ Arrears of Annual Contributions		40	0	0	
„ Annual Contributions for year		2125	10	0	
Do. in advance		32	0	0	
					2197 10 0
„ Composition Fees					46 0 0
„ Interest on Investments (including Income Tax recovered).....					253 14 11
Do. Deposit					2 9 2
Do. Post Office Savings Bank Account					32 6 1
„ Sales of Publications:—					
Transactions		10	13	4	
Journals		17	14	5	
Proceedings		8	11	3	
History of the Society			3	9	
Miscellaneous			9	9	
					37 12 6
„ Donations in aid of Publications					100 0 0
„ Donation for General Purposes					3 4 4
„ Miscellaneous Receipts					29 13 11
„ Redemption of £1,000 4½ per cent. Conversion Stock .					1000 0 0
					£4689 18 4

	RECEIPTS	£	s.	d.	Library
		£	s.	d.	£ s. d.
To Balance 1 May 1940.....		268	1	9	
„ Interest on Investments (including Income Tax recovered)		46	1	2	
„ Sales			2	7 10	
„ Redemption of £88 9s. 8d. London County 5 per cent. Stock (Stebbing Bequest)		88	9	8	
„ Deposit Account Interest				7 1	
					£405 7 6

	RECEIPTS	£	s.	d.	Fellows Postal
		£	s.	d.	£ s. d.
To Balance at 1 May 1940		51	0	3	
„ Deposits during year			4	0	
					£51 4 3

YEAR ENDED 30 APRIL 1941.

Meeting, 24 May 1941.)

from 1 May 1940 to 30 April 1941.

Account

	PAYMENTS	£	s.	d.	£	s.	d.
By Coal, Electric Current, and Gas.....					93	3	5
„ Window Screens					55	10	9
„ Repairs: Sundry					14	7	10
„ Taxes and Insurance					55	5	0
„ Miscellaneous Printing and Stationery.....					35	15	1
„ Petty Expenses and Postages					140	7	1
„ Publications:—							
Printing	335	14	4				
Illustrations.....	23	4	9				
Distribution.....	20	8	3				
					379	7	4
„ Salaries and Wages, etc.					1161	6	6
„ Zoological Record Donation					15	0	0
„ Purchase of £50 0s. 0d. 3 per cent. Savings Bonds (Investment of Composition Fee)					50	0	0
„ Linnean Medal.....					17	15	6
„ Herbert Spencer Bequest:							
Cost of Removal of part of Library					27	10	0
„ Purchase of £1,000 0s. 0d. 3 per cent. Defence Bonds .					1000	0	0
„ Balance at 30 April 1941:—							
Current Account at Bank.....	241	8	11				
Deposit Account Post Office Savings Bank	1156	5	3				
Deposit Account Post Office Savings Bank (Herbert Spencer Bequest)..	243	14	9				
Cash in hand	3	0	11				
					1644	9	10
					<u>£4689</u>	<u>18</u>	<u>4</u>

Account

	PAYMENTS	£	s.	d.
By Books		5	5	6
„ Periodicals.....		40	8	5
„ Binding		71	16	8
„ Balance at 30 April 1941: Current Account	137	16	11	
Deposit Account	150	0	0	
		287	16	11
		<u>£405</u>	<u>7</u>	<u>6</u>

Account

	PAYMENTS	£	s.	d.
By Postages etc. during year		17	2	
„ Balance at 30 April 1941		50	7	1
		<u>£51</u>	<u>4</u>	<u>3</u>

Separate Account

RECEIPTS

To Balance at 1 May 1940 :—			
Westwood Fund	£53	14	11
Trail Award Fund	18	19	2
Crisp Award Fund	22	6	10
Hooker Lecture Fund	76	3	3
Goodenough Fund	6	11	11
Minchin Fellowship Fund	10	15	0
	188	11	1

Interest on Investments (including

Income Tax recovered) :—

Westwood Fund	£11	14	1
Trail Award Fund	3	10	0
Crisp Award Fund	10	4	8
Hooker Lecture Fund	22	9	11
Goodenough Fund	9	4	4
Minchin Fellowship Fund	5	17	6
Staff Pension Fund	54	5	4

Redemption of £100 0s. 0d. London County
5 per cent. Stock (Minchin Fellowship
Fund)

£405 16 11

PAYMENTS

By Crisp Award Fund; Award and Medal	£	s.	d.
„ Westwood Fund; Cost of Illustrations	20	19	6
„ Minchin Fellowship Fund :—	37	5	9
Transferred to Annual Contributions	4	0	0
„ Staff Pension Fund :—			
Purchase of £52 18s. 5d. 3 per cent.	52	15	4
Conversion Stock			
Purchase of £1 9s. 9d. 3 per cent.	1	10	0
War Stock.	54	5	4

Balance at 30 April 1941 :—

Westwood Fund	£28	3	3
Trail Award Fund	22	9	2
Crisp Award Fund	11	12	0
Hooker Lecture Fund	98	13	2
Goodenough Fund	15	16	3
Minchin Fellowship Fund	112	12	6

289 6 4

£405 16 11

General Account

£	s.	d.	£	s.	d.
3½ per cent. London County Consolidated Stock 1958-68	1000	0	0	1040	0
India 3 per cent. Stock	1200	0	0	87½	0
Eastern Bengal Railway 4 per cent. Irredeemable Debenture Stock	1000	0	0	1050	0
Great Western Railway 4 per cent. Debenture Stock	1000	0	0	99½	0
London Midland & Scottish Railway 4 per cent. Preference Stock	1000	0	0	109½	0
3½ per cent. War Stock	312	0	0	166	18
3 per cent. Defence Bonds	338	6	8	350	3
4 per cent. Australian Stock 1961-64	1000	0	0	1000	0
3 per cent. War Stock 1955-59	2199	18	6	2353	18
3 per cent. Savings Bonds 1955-65	200	0	0	201	0
	50	0	0	50	0
				£8302	0

Library Account

£	s.	d.	£	s.	d.
North Bridge Railway 4 per cent. Stock (Bentham Bequest)	450	0	0	91½	0
East Indian Railway 3½ per cent. Debenture Stock (Tagart Bequest)	530	0	0	506	3
Surrey County 3 per cent. Stock 1961-66 (Wakohurst Bequest)	103	12	5	98	8
4 per cent. Australian Stock 1961-64 (Walker & Morey Bequests)	191	12	7	205	0
				£1221	7

Separate Account

£	s.	d.	£	s.	d.
Metropolitan Water Board 3 per cent. "B" Stock (Westwood Bequest)	232	5	0	87½	4
Ditto	667	14	2	584	4
Ditto	163	11	5	143	2
New South Wales 3½ per cent. Stock, 1930-50 (Trail Award Fund)	100	0	0	87½	0
2½ per cent. Consolidated Stock (Crisp Award Fund)	409	11	1	100	0
India 3½ per cent. Stock 1931 (Westwood Fund)	129	10	11	317	8
Ditto	61	18	0	128	17
Ditto	123	15	11	61	11
3½ per cent. Conversion Stock (Staff Pension Fund)	1547	8	7	123	3
3 per cent. War Stock 1955-59 (Staff Pension Fund)	101	9	9	1613	3
				101	11
				£3376	16

F. C. STERN, Treasurer.

We have (in conjunction with the Professional Auditor, who certifies as to all details) audited the Accounts of the Society for the year ended 30 April 1941, and found them correct. We have verified the Investments and Bank Balances.

Dated this 20 May 1941.

W. B. KEENE, Chartered Accountant,
23 Queen Victoria Street,
London, E.C. 4.

E. S. RUSSELL, J. E. DANDY,
I. H. BURKILL, ANNA B. HASTINGS,
R. H. BURNE, D. M. REID,
MALCOLM SMITH.

Audit Committee.

PRESIDENTIAL ADDRESS.

By E. S. RUSSELL, O.B.E., M.A., D.Sc.

BIOLOGICAL ADAPTEDNESS AND SPECIALIZATION OF INSTINCTIVE BEHAVIOUR.

I propose in my Presidential Address to consider some aspects of the problem of instinct, treated deliberately from a psychological and biological point of view, as distinct from a physiological. I regard animals not as mechanisms actuated by stimuli, but as feeling, perceiving and striving subjects. This is, I hold, a legitimate and useful hypothesis. In particular I make the assumption that animals do actually sense and perceive certain aspects of their environment, and act with reference to these sensations or perceptions; each accordingly lives within a sensory or perceptual world which is private to it. I shall pay particular attention to the perceptual side of instinctive behaviour.

I call *valent*, or possessing *valence*, those objects and events in an animal's extero- or interoceptive field to which it attends and in respect of which it shows behaviour, or action directed towards an end or end-state (Russell, 1938). This definition is a neutral one, inasmuch as it does not indicate the characteristics of valent objects and events. But it is implicit in the definition that we can judge of valence only from behaviour; that to which no response is made possesses no valence, is not attended to, and is in effect not actively perceived. And from the kind of behaviour manifested towards a valent object or event we can infer the general nature of its valence. In any behaviour-act we can determine by observation and experiment the end or end-state towards which it is aimed; it may be the finding of food or a mate, it may be escape from enemies by flight or concealment, it may be oviposition. We can therefore say that sensations and perceptions eliciting food-getting behaviour have food-valence, those eliciting flight danger-valence, those leading to egg-laying oviposition-valence, and so on. Valences are therefore in general characterized functionally; they represent in practice values or meanings for the animal, and it is essentially to the meaning or significance of its sensations or perceptions that an animal responds. It is, in fact, valences that the animal psychologist should study rather than sensations and perceptions *per se*. It is unnecessary to assume that the animal is consciously and explicitly aware of the meaning of valences, but it acts as though it were. The important fact is that the valent sensations and perceptions to which the animal responds instinctively are, usually, meaningful in relation to its vital needs and requirements.

That is to say, objects having for a particular species danger-valence are usually dangerous to it, objects with food-valence are normally suitable food for it, those with oviposition-valence normally suitable for the development of its eggs, and so on.

I propose to illustrate in some detail this general truth that an animal is instinctively attuned to attend to, perceive and act with reference to certain aspects of, or events in, its environment, which are normally objects or events that are biologically significant for it. There is an innate disposition to act in an adequate way with respect to these particular valent phenomena and to respond to no others, save such, of course, as acquire valence through experience and learning*. We can best approach this study of the adaptive specialization of instinctive perception by considering the biological basis of instinctive behaviour.

Instinctive behaviour is to be regarded, from the biological point of view, as one of the means through which the animal fulfils the biological ends of development, maintenance and reproduction. Now as each species of animal fulfils these ends in a particular way, being after its kind a functional and ecological specialist, we may expect to find that its instinctive equipment, its predisposition to particular perceptions and actions, is also specialized and adapted to its functional requirements, and to the particular environmental complex in which the species normally lives, at different stages of its existence.

It is usual to think of 'adaptation' or adaptive specialization in terms especially of the visible 'characters' of the animal such as its protective coloration. But this is clearly a very superficial view. It is, quite obviously, the animal as a living entity, throughout its entire life-cycle, including reproduction, that is 'adapted' to environment, and if a sufficient number of individuals were not so adapted, the species could not survive.

Adaptation, or adaptive specialization, is therefore not simply a matter of superficial 'characters,' such as may be supposed to have 'survival value,' but of the behavioural, physiological and morphogenetic activities of the animal throughout its whole life-cycle. Adaptive specialization rules throughout the whole life history—in the conditions of fertilization, of embryonic or larval life, of the reproductive functions, as well as in the maintenance activities of the adult. There must be no weak link in the chain, otherwise the species disappears.

Let me illustrate what I mean by considering the main points in the life history of parasitic Hymenoptera (Families

* I deal throughout with pure instinctive behaviour, unmodified by learning, or 'conditioning'.

Chalcididae, *Braconidae*, *Ichneumonidae*.) These insects have taken up a highly specialized mode of existence, have occupied a very special ecological niche, for they pass their larval stages in the living bodies of various insect hosts, parasitizing them in the caterpillar or chrysalis stage and in some cases in the egg itself.

If the parasite species is to survive, the sexes must be able to find one another and effect the fertilization of the egg; the female must be able to find and oviposit in a suitable host—a host in which her larvae can survive and develop. She must have the necessary organ for inserting her egg into the body of the host, a sharply pointed ovipositor, and the impulse to plunge it in. In its turn, the larva must be adapted in structure and physiological functioning to live and grow in the very special conditions afforded by the interior of the host. That it is so adapted and specialized is well illustrated in the excellent description given by Cameron (1938) of the larva of the Ichneumon *Glypta haesitator*, a parasite of the caterpillar of the pea-moth *Cydia nigricana*, in which he calls special attention to the adaptations in the cephalic skeleton and jaws. This apparatus is more developed in the first and fourth stage larvae than in the second and third; in the first stage it is required for the act of eclosion from the egg, and in the last stage for feeding on solid food. 'In the earlier stages,' he writes, 'the parasite larva obtains nutriment in a fluid condition, but in the last instar it has to live mostly on solid food, consisting of the remaining tissues of the host, such as the fat-body, etc., and for this work it requires stronger mandibles and a stronger supporting skeleton. Stronger mandibles are also useful when the time comes for it to break through, and cast off, the skin of its host. The arduous task of cocoon spinning is carried out in this stage. This latter function is specially provided for by the transformation of the salivary gland and its opening into a silk gland and a spinneret, respectively. . . In the second and third stages the cephalic skeleton is present, but the parts are only weakly chitinized, from which it would appear that it has no special function to perform save that with each moult the parts get successively larger in preparation for the work awaiting them in the final stadium' (p. 292).

Here we have an excellent example of that proleptic or anticipatory formation of special structures to meet coming needs which is so striking a feature of the directive process of development. And it seems clear that without these special provisions, and many others of an adaptive kind, the larva could not successfully carry through its development.

Turning now to the behavioural adaptations concerned in the finding of a suitable host, we see at once their vital

importance for the continued existence of the species. From the very fact that a parasite species continues to exist we can infer that a sufficient number of females manage regularly to find and oviposit in suitable hosts. They must have, therefore, the impulse to seek for such hosts, and the power to recognize them in some way, by their specific smell, or by their size and shape and texture, or by some other characteristic. Every species that persists and maintains itself successfully must be, as regards its females, biologically adapted and specialized to find and parasitize a host or hosts in which its offspring can develop normally. Some species limit themselves to a single kind of host; others successfully parasitize a large number. There are, therefore, degrees of specialization or restriction. It may well be that in the case of a species normally restricted to one particular kind of host the larvae could develop successfully in a wider range of hosts*—specialization may go further than adaptedness requires—but the fact remains that the species is adjusted or specialized instinctively to seek out one particular host.

Let us consider the nature of this instinctive predisposition. It seems unreasonable to suppose that the ovipositing female is guided in her choice by explicit knowledge that such and such a host is a suitable one for the development of her egg, and acts with intelligent purpose. She knows nothing of her egg *qua* egg, i.e. as something which will develop into a larva and adult; it is to her merely 'something to be laid'. She can know nothing of the nutritive relations that will be set up between her larva and the host. It seems inconceivable that the female can have such knowledge; she is an insect, not an entomologist. And the fact that instinct can err and is easily led astray in abnormal or unusual situations is sufficient to show that no supernatural faculty of direct intuitive knowledge is involved, as Bergson would have us believe.

We see then that instinctive behaviour is not a matter of the intelligent and purposive pursuit of ends; it is a matter of specialized and pre-adapted capacity—the capacity or predisposition to perceive certain things and events, and to act in a particular manner with reference to them. It knows

* Evidence of this is available for some of the hunting wasps, which normally provision their nests or burrows with one kind of prey. *Odynerus callosus* in natural conditions brings only one or two kinds of caterpillar to her nest; Balfour Browne, however, found by experiment that almost any kind of insect or spider material, if it was soft enough, was readily eaten by the larvae (1925, p. 54.) Howes (1919) was able to bring up the larvae of the forest shell-wasp (*Zethousculus humatus*) on spiders, though their normal food is small caterpillars. Also in Nature there may be considerable variation in the food supplied; the Pompilid wasp *Pseulagenia carbonaria* usually provides spiders for her larvae, but Mequignon (1938) has observed her filling her nest with earwigs.

what to do about them, though it does not know why. As Spaier (1930) has well said, instinct is characterized by 'savoir-faire', as distinct from 'connaissance'. The normal purposiveness of instinctive behaviour is due to biological pre-adaptation and specialization, and not to intelligence.

Instinct is specialized on the perceptual side as much as on the executive. The female having the instinctive disposition to seek out a particular host must be guided by some perceptual clue which is normally associated with that host alone, and this clue may be both simple and normally adequate—a specific smell for example, associated with an object of a certain size and shape.

The Chalcid *Microplectron fuscipennis*, for instance, is restricted in her attacks to the resting larva of the saw-fly *Diprion*, which is enclosed in a cocoon (Ulyett, 1936). She does not, however, seek what we think of as 'a cocoon of *Diprion*'; she cannot form a concept such as this; she seeks simply an object (or manipulandum, as Tolman would call it) which is attractive to her as 'something to be pierced' with her ovipositor, an object that has this particular functional valence.

She must be able to distinguish this object from other similar objects, by means of a few sensory characteristics, such as smell, shape and texture (see p. 262), which are not necessarily those which we perceive as diagnostic of a *Diprion* cocoon. She is, in a word, adapted and specialized in her sensory capacities in such a way as to perceive and be attracted to certain specific objects (which are biologically suitable for the development of her eggs), and to be impelled to oviposit in them, in preference to other similar objects. Such objects alone have for her oviposition valence.

This specialization and adaptedness of instinctive behaviour on the perceptual as well as on the executive side is obviously just one aspect or expression of the adaptive specialization which characterizes the individual and the species as a whole.

Correlative with the fact that animal species are adaptively specialized is the fact that they normally live in a more or less definite and specialized environment or ecological norm, which is optimal for their vital requirements. This may be extremely restricted, as in the case of caterpillars that feed on one kind of plant, or live in a specialized environment, as do the leaf-miners; or it may be very wide, as in the case of many far-ranging birds and fishes. It is impossible to define it except in terms of the functional needs and requirements of the species, with which it is correlative. It may alter radically in the course of the individual life; many teleostean fish completely alter their habits and habitat when they change over from a free-floating planktonic existence to a life

on the bottom of the sea, and drastic changes in life-habits and the ecological norm are notoriously shown by holometabolic insects.

It is a very interesting problem of animal behaviour to determine how a species finds and remains in the ecological norm appropriate to each particular stage of its life. This is too big and comprehensive a question to be tackled here in detail, but I propose to consider in outline some of the ways in which animals contrive to lay their eggs in the special ecological norm which is suitable for their development, and I do this in order to illustrate still further the adaptive specialization of instinctive behaviour, both on the perceptual and on the executive side.

In the simplest case, the animal deposits its eggs within its own ecological norm; the pond-snail *Lymnaea*, for instance, lays its gelatinous masses of eggs on the vegetation of its home pond; many shore fish, like the blennies and gobies, fix their eggs in crevices of the rocks within their normal habitat. But it often happens that the ecological norm for the eggs and larva is quite different from that of the adult; especially is this the case with insects that undergo metamorphosis, and with marine animals that have pelagic larvae. In such cases the female usually selects for oviposition either the ecological norm required by the larvae or a place from which this norm can be reached. An insect, for example, may oviposit directly on the food plant of its larva, or on the substance, such as dung or carrion, on which the larva feeds. If it has an aquatic larva it may oviposit on the surface of the water, like many dragonflies, or it may insert its eggs in plants growing in or near the water. Many marine fish normally spawn up-current, in such a position that their floating larvae are usually drifted down towards an area in which they find suitable conditions for their later development and growth (Russell, 1937).

Here are two examples of the selection by insects of the general environmental conditions required by their larvae. A species of tse-tse fly, *Glossina palpalis*, found on the shores of Victoria Nyanza, feeds by preference on reptilian rather than mammalian blood; it is most numerous on the open beach and banks of streams which crocodiles and *Varanus* frequent. Here also are found its pupae in greatest numbers, adjacent to the food supply when they hatch out. Hale Carpenter (1934) made a careful study of the exact locations where the females deposited the mature larvae they produce. He concluded that they sought out with great accuracy areas of loose dry soil, well shaded, with a surface exposed to the air, within a few yards of high water-mark, but beyond the reach of the water.

Similar care in the selection of a suitable place in which to lay her eggs is exhibited by the flying imago of the ant-lion, *Myrmeleon formicarius*. On warm summer evenings in the twilight the females are to be found flitting round the sun-warmed sandy spots where were situated the funnels in which they lived as larvae (Doflein, 1916, p. 128), and in these areas they deposit their eggs. These spots must be warm and dry and sunny, preferably sheltered from the rain by an overhanging bank or tree, and floored with sand or dust in which the larvae can dig their conical funnels. If the female chooses an unsuitable spot, the larvae on hatching will move about till they reach their proper ecological niche, guided by light and temperature, their responses to which are such as to lead them to the proper spot.

Selection of a position for egg-laying from which the young will normally reach their ecological niche is well illustrated by the cicadas. In their immature state, which may last for many years, as in the famous 'seventeen-year locust', these insects live underground, in narrow vertical shafts, getting their food by sucking the juices of roots. When the time comes for metamorphosis, the nymphs emerge from their burrows in the late spring, and immediately seek out some plant or tree, which they climb and to which they cling, while they burst out of the nymphal shell as fully formed imagos. *Magiccicada septendecim*, according to the careful investigations of Andrews (1937), treks steadily and persistently towards the nearest tree—which it perceives visually, not as a complex thing such as a tree appears to us, but 'as an area of greater or less light contrasted with the background'. If it is prevented from reaching a tree it will climb up some other vertical object, like the palings of a fence, chicken wire, or tall grass stems, and metamorphose on them. 'If it encountered a man lying down', writes Andrews, 'it surmounted him and walked on over him to the tree, but if the man were standing up beneath the tree the cicada might climb up him and even transform fastened to his clothing, without reaching the tree' (p. 281). So what this species of cicada seeks is not 'a tree', but some vertical object, standing out against the visual background, which it must climb. In natural and normal conditions this object is, generally, a tree, and for another purpose, that of oviposition, a tree is for the female the biologically suitable object. This is reached through very simple, but normally adequate behaviour—behaviour adapted to a normal environment, which contains more trees than, for example, posts.

All the kinds of cicada insert their eggs in the tissues of plants, to the number of several hundreds, either in the twigs and branches of bushes and trees, or in the stems of herbs or grasses. They are not very specific in their choice, though

the European *Tibicen plebeia* often selects the dry stems of the asphodel for oviposition. With respect to *M. septendecim*, Andrews tells us that they 'commonly work upon twigs of about the thickness of a lead pencil and often of last year's growth. When they use smaller twigs this frequently works disaster, as the twig breaks off and hangs with dead leaves or falls to the earth' (p. 287), and the eggs laid therein do not develop. Sometimes cicadas will lay eggs in quite unsuitable places; *Melampsalta cingulata* has been known to oviposit in an apple (Myers, 1929, p. 106), *Tibicen erratica* in the boards of a shed-roof, and on the handles of hoes left standing during the dinner hour. More remarkable still, *M. septendecim* has been seen trying to insert eggs in the iron rod of a bridge, extruding seven.

These scattered observations suggest that the instinct of the female when ready to lay is simply to climb upwards; normally this means climbing up a tree or a bush or a stem, and normally this action will lead her to a suitable site for oviposition. When she comes across man's handiwork her instinct to ascend does not lead her to a suitable spot—but she oviposits all the same. Instinctive behaviour is adapted to the normal or most usual situation to be encountered by the species, and takes no account of the unusual.

The cicadas do not lay their eggs in the ecological niche inhabited by the larvae or nymphs, which, as we have seen, is underground, in proximity to the roots of trees and other vegetation on which they feed. They lay the eggs, however, in places from which this habitat can be reached by the simple device of falling to the ground and burying. The larvae hatch out as tiny sheathed nymphs, the size of a flea, and climb out of the egg-nest towards the light, moving outwards or upwards to the ends of the twigs; then, after a varying period of time, a quarter of an hour to several hours, they let themselves fall to the earth, where they immediately creep down any crevice or actually dig themselves in.

Snodgrass (1921) gives the following description of the behaviour of newly hatched *Magicicada septendecim* which he placed in a pan of earth. 'These at once proceeded to get below the surface. They did not dig in, but simply entered the first crevice that they met in running about. If the first happened to terminate abruptly, the nymph came out again and tried another. In a few minutes all had found satisfactory retreats and remained below. The avidity with which they dived into any opening that presented itself indicates that the call to earth is instinctive and imperative with them once their feet have touched the ground' (p. 408). Andrews (1937) describes how the newly hatched nymphs of the same species squeeze themselves into crevices and cracks in the

ground, fall down or climb down the holes left by their parents on emergence from their seventeen years' sojourn below ground: he found that they could actually dig into the ground, slowly but surely.

Active burrowing has been observed also by Fabre and by Myers. Fabre's specimens (*Tibicen plebeia*) ran around for two hours before burying: when they were dug up they re-buried themselves immediately. Myers' young nymphs of *Melampsalta leptomera* placed on moist sand buried at once, twelve disappearing under the surface in ten minutes: after twenty-four hours some were three inches down.

Another example of oviposition in a place from which the newly hatched insect can, usually, reach its ecological niche is afforded by the dragonfly *Lestes viridis*, whose larva is, like those of all dragonflies, aquatic. The female lays her eggs in the autumn on the underside of willow or osier stems, forming galls. In the spring the larva hatches out, enveloped in its pro-nymph sheath. By a strong bending of the body it jumps clear of the stem, and usually falls into the river. If, however, it falls on to the ground, it skips vigorously about until, aided by the slope of the ground towards the river, it eventually jumps into the river (Tillyard, 1917, pp. 72-3). There it floats back downwards until it emerges from its sheath and takes up life on the bottom.

Deposition of eggs directly on the food-plant or on other objects or substances suitable for the growth of the larvae is, of course, a widespread phenomenon in insects. Here are a few examples.

In the Lepidoptera the female generally lays her eggs on the food-plant or plants of the larva, and this is often found by its smell. The following examples I take from Hering's book (1926).

The goat moth *Cossus ligniperda*, whose caterpillars live in the woody tissues of willow and other trees, seeks out injured parts of the trunk on which to lay her eggs. The wound tissue, being rich in nutritive substances, forms a good spot for the larva to begin life, and from such spots it later burrows into the wood. Generally fermentation occurs at the wound, with production of acid and a characteristic smell. It is this smell that attracts the moth. One has been observed to settle down on a streak of vinegar on the tree trunk and attempt to find the wound in which to lay its eggs.

The butterfly *Papilio demoleus* normally oviposits on the orange tree. It has been seen to lay eggs on various plants and on the ground to leeward of a strongly scented tree, these being so strongly impregnated by the smell as to be for the butterfly functionally equivalent to the parts of an orange tree.

Females of the moth *Acronycta auricomata* kept in a box with their food-plants were found to lay, not on the plants, but on the sides and bottom of the box, which was presumably impregnated with their smell. A similar state of affairs was found by Thompson and Parker (1928) when studying host selection in the corn-borer *Pyrausta nubilalis*; females confined in cages with their food-plant laid a considerable proportion of their eggs on the woodwork and the plant-pots. These observations suggest that the chief valent characteristic of the food-plant is its smell.

The fruit-fly *Drosophila ampelophila* lays its eggs in fermenting fruit, which it finds by smell. The experiments of Barrows (1907) have shown that it exhibits an optimum response to a mixture of ethyl alcohol of 20 per cent. and acetic acid of 5 per cent., which are about the strengths found in the fermented apple juice.

A very interesting case has been described by Fräulein Ilse (1937), from which it appears that the female cabbage white butterfly *Pieris brassicae* may be guided in part by colour sense in finding the cabbage and other plants on which it lays its eggs. When hungry, these butterflies give a specific feeding response to red, yellow, blue and violet colours such as occur in flowers; when they are set on egg-laying, however, they give a peculiar 'drumming reaction' with the first pair of legs, and this is elicited by any object which shows colours ranging between emerald green and greenish blue. During this phase yellow and pure blue colours are disregarded; the drive to egg-laying shifts attention to greens and greenish blues, characteristic of the leaves on which it normally oviposits.

A similar case was described by Knoll in 1922, whose observations are summarized by Bodenheimer (1938) as follows:— 'The colours to which the hawk-moth *Macroglossa stellatarum* is attracted, change, in the gravid female, to that of chlorophyll, and this attraction, coupled with the smell of etheric oils of *Galium*, guarantees the proper oviposition and development of the caterpillars' (p. 48).

Regarding the choice of suitable hosts for their eggs by the parasitic Hymenoptera and Diptera, a great deal of interesting work has been done, especially in the field of applied entomology. These insects lay their eggs in, or on, a great variety of Arthropod, chiefly insect, hosts, and their choice of a host may be highly specific, being limited to a particular stage—egg, or caterpillar or pupa—of one species or of a narrow range of species. The Chalcid *Ooencyrtus kuvanae*, for example, limits her attacks principally to the eggs of the gypsy moth *Porthetria dispar*, though in the laboratory she will parasitize the eggs of eight other species of Lepidoptera (Lloyd, 1938).

Or the species may be 'polyphagous', attacking a wide range of hosts; *Compsilura concinnata*, a dipterous (Tachinid) parasite, injects its living larvae into caterpillars of more than fifty species, including saw-fly 'caterpillars'.

But whether the choice is wide or restricted, the hosts chosen are in general such that the young can develop successfully in them; the choice is adaptive—and may be highly specialized.

Evidence that a parasite species in natural conditions rarely oviposits in a host unsuitable for its progeny has been collected by Thompson (1939). He has examined many thousands of hosts of all kinds, and has found that, with insignificant exceptions, they contained only parasites which are known to be capable of development in the hosts in which they occurred. The evidence indicates, he concludes, 'that the choice of the host by the parasite is, in general, both *specific* and *adaptive*. The parasite is restricted to certain kinds of hosts; these kinds are, generally, the kinds suitable for the offspring' (p. 355). The instinctive activities of the parasitizing female are, therefore, like most instinctive actions, both adapted and specialized. In normal and natural conditions the parasite will usually choose the right or biologically adequate host. Selection, however, is not infallible, and errors may be made. In abnormal conditions, as when it is prevented from access to its normal hosts, it may oviposit in hosts or in objects which are unsuitable (see later). That unsuitable hosts are not infrequently attacked both in experimental and in natural conditions is maintained by Salt (1938), but such faulty behaviour must clearly be the exception in natural conditions, and not the rule, otherwise the species would die out.

How does the insect, in natural conditions, find a certain kind or kinds of hosts? We cannot suppose that it knows by intellectual process that such and such hosts are suitable, and we have no reason to think that instinct is a magical faculty which gives the animal intuitive insight into the nature of things. It seems, then, as I have indicated before, that the insect must be guided by perceptual clues, to which it is predisposed or pre-adapted to respond, and that these clues, or 'sign posts', as Thompson calls them, are normally adequate to indicate the suitable object.

Let us consider now some of the perceptual clues or valent characteristics by which these insects are guided in their choice of a host. In some cases they are attracted primarily by the locality in which the host is normally to be found. The Braconid *Alysia manducator* parasitizes several kinds of insect larvae that live in decaying carcases. The experiments of Laing (1937) show that the primary attraction is the smell

of fresh or decaying meat, which leads the insect to the place where the maggots are likely to be ; they are found by stabbing movements of the ovipositor as *Alysia* walks about on the carcase. The Chalcid *Mormoniella vitripennis* oviposits in the pupae of carrion-feeding flies ; it also is attracted primarily by the carrion environment of the pupae, rather than the pupae themselves. It is noteworthy that *Mormoniella* is little attracted by the smell of fresh meat, but powerfully by the stink of meat nine days old, while *Alysia* responds markedly to the smell of fresh meat. The difference in valence of fresh meat is correlated with the fact that *Alysia* parasitizes larvae, *Mormoniella* pupae.

The minute Chalcid *Trichogramma evanescens* parasitizes the eggs of many kinds of Lepidoptera and, according to Laing, (1937) appears to find these objects at short range by sight ; it is attracted also to sand-grains. Her experiments show that while the smell of the eggs themselves is not important, *Trichogramma* is attracted to, and searches, areas where the parent moths have left chemical traces of their presence. The acceptability of the egg when found is determined by tactile exploration with the antennae.

Other examples of attraction to the immediate environment of the host are given by Thompson in the paper of 1939 to which I have already referred. When studying, in conjunction with H. L. Parker, the Ichneumonid *Eulimneria crassifemur*, which attacks the European corn-borer grub, he noted that it was roused to activity by fragments of the corn plant, and explored the material with its ovipositor if corn-borer larvae had been feeding on it. Reference may also be made to the work of Thorpe and Caudle (1939), who found that the females of the Ichneumon *Pimpla ruficollis* bred in larvae of the pine-shoot moth are attracted, when mature, by the odour of *Pinus sylvestris* oil, though in the early part of their lives, when they feed on umbelliferous flowers, they are repelled by it. This is an interesting example of change of valence related to the ripening of the gonads—a phenomenon we have already noted with regard to colour sense in *Pieris* and *Macroglossa* (p. 259 above).

In the finding of the host's environment, olfactory sense seems to play an important part, and the same is often true of the finding of the host itself. For example, the parasitic hymenopteron *Habrobracon juglandis*, which oviposits in the caterpillar of the flour moth *Ephestia kühniella*, appears to find its host exclusively by smell (Murr, 1930). The specific scent of the caterpillar is sufficient to elicit the actions—bending of the abdomen and extrusion of the ovipositor—preliminary to egg-laying. It will exhibit this behaviour on a glass plate rubbed with the skin of an *Ephestia* caterpillar

as well as when following the scent-trail of a living caterpillar. It pays no attention to an *Ephestia* caterpillar sealed down under a glass capsule, nor to models made of plasticine or cotton wool. On the other hand it will pierce these models with its ovipositor if they are smeared with *Ephestia* juice, and also dark-coloured beetle larvae similarly treated. Oviposition is, however, not completed in these substitute objects.

(It is to be noted that in these, as in other experiments, the proof that the smell is quite specific is lacking. Possibly other caterpillars of similar smell might elicit oviposition. The range of valence has not been determined.)

Specific smell appears to induce the preliminaries of oviposition in the Ichneumon *Pimpla instigator*, which parasitizes the pupa of *Pieris brassicae*, for it will pierce with its ovipositor paper soaked in the blood of the chrysalis of this species (Picard, 1922). No actual oviposition, however, takes place.

Specific smell may be only one of the valent characteristics of the host, as our next example shows.

The Chalcid hymenopteron *Microplectron fuscipennis* parasitizes the resting larva of the saw-fly *Diprion*, which is enclosed in a compact cocoon, laying many eggs in each victim. It is restricted to this genus for a host, laying in no other. From his experimental work, Ulyett (1936) concludes that the normal course of events when *Microplectron* seeks a host is as follows. In its traverse of the area it may come across the cocoon by chance, but the primary valent characteristic appears to be the specific smell of the larva, which according to laboratory experiments exercises an attraction at a distance of 5 to 6 mm. If the object smells right it is mounted and examined by the antennae. In the laboratory an object with edges, such as a rectangular piece of pith, is rejected in favour of an object with rounded contours. Size, within limits, does not seem to be important, but texture may be. In natural conditions, of course, an object which smells right and has the shape and contour of a cocoon is bound to be the cocoon of *Diprion*.

The proper object having been found, oviposition follows, provided that the larva is alive and is not full of advanced grubs from a previous parasitization. If it contains eggs or very young grubs the finder may parasitize it again. How *Microplectron* discriminates between these two states of the *Diprion* larva is not quite clear. It may be through a different smell, or, as Ulyett is inclined to hold, through perception of the movements of the healthy or recently parasitized larva. In experimental conditions, if no adequate object is present, *Microplectron* may attempt to oviposit in a biologically inadequate object, such as a gelatine capsule of approximately the same size and shape as a *Diprion* cocoon, responding mainly

to the valent characteristic of shape ; but this is unlikely to occur in Nature.

To *Microplectron*, then, its host is a visual and tactile object or 'manipulandum' characterized primarily by a specific smell, and secondarily by shape and, possibly, texture. Other valent characteristics determine whether the object shall be pierced by the ovipositor and eggs laid in its interior substance.

The minute Chalcid *Trichogramma evanescens*, which is a polyphagous egg-parasite, appears to choose hosts mainly by size, and, to some extent, shape. In laboratory conditions, according to Salt (1935), it may select, in preference to the small eggs of the moths *Sitotroga* and *Ephestia* in which it can develop successfully, such unsuitable objects as seeds, grains of sand, fragments of glass, or globules of mercury, which are larger than itself, and try to oviposit in them. In such conditions, selection purely on a basis of size leads the insect astray. In natural conditions, when *Trichogramma* is actively searching for its hosts in the open on various kinds of vegetation, selection on a basis of size (and shape) should normally lead to successful oviposition, for the most common objects of such size in the environment which is searched are likely to be insect eggs, as Lloyd (1938, p. 319) points out. The perceptual clues of size and shape are thus normally adequate, though in a very rough and ready sort of way.

Salt has made a most interesting analysis of the valent characteristics which lead to oviposition. Objects attacked must protrude above the surrounding surface ; they must not be wet or sticky, or in motion, and they must be firm enough for the *Trichogramma* female to mount upon them. They must fall between certain limits of size, and must not be too elongated—"in brief, to be acceptable to *Trichogramma*, a host must be of such a shape and size, that is of such dimensions, that it could contain the parasite" (p. 431). Surface texture, colour and smell are unimportant.

In his paper of 1938 he gives a striking example of specialization in instinctive behaviour as between two almost indistinguishable species of *Trichogramma*—*T. evanescens* and *T. semblidis*. The latter will attack and successfully parasitize the eggs of the alder-fly *Sialis lutaria*, which are laid in close masses containing several hundred eggs. *T. evanescens*, on the other hand, cannot be induced to attack these egg-masses, but if the eggs are separated from one another it will attack and parasitize them ; the larvae, however, do not develop well, and only a few feeble and defective adults are produced. *T. semblidis* is, therefore, biologically adapted and specialized for successful reproduction in the eggs of *Sialis* and is psychologically predisposed to attack the egg-masses of this insect.

Insect parasites not only select as a rule hosts which are suitable for their progeny, but also, in some cases, they discriminate between hosts that have already been parasitized and hosts that have not. The biological adaptedness of such action is obvious, for the host, especially if it is an egg, provides only a limited amount of food, and only one or a limited number of parasites can develop successfully in it. This was first discovered by Salt (1932) with respect to the Ichneumonid *Collyria calcitrator*, and in later work on *Trichogramma* (1937) he concluded that the basis of the discrimination was the contact-odour left on the egg by a previous female; eggs so contaminated would normally be eggs already parasitized. Ulyett, as already mentioned, found that *Microplectron* would not oviposit in cocoons of *Diprion* containing advanced larvae resulting from a previous parasitization.

A remarkable power of discrimination has been demonstrated by Lloyd (1938) in the Chalcid *Ooencyrtus kuvanae*, an egg-parasite of the gypsy moth *Porthetria dispar*. In carefully controlled laboratory experiments he found that *Ooencyrtus* would almost invariably select unparasitized eggs if given a choice between these and eggs containing one or more parasite eggs. If it is compelled to superparasitize, being given only gypsy moth's eggs containing parasite eggs or parasites at various stages of development, it selects those eggs containing the youngest parasite stages. The response is a graded one, and shows all the features of the well-known phenomenon of 'relative choice' which has been demonstrated in various mammals and birds. The basis of discrimination is not certainly known, but 'it is suggested that the graded oviposition response of the females towards hosts containing advanced developmental stages of the parasite may be conveniently correlated with the decreasing quantity of actual host material present within the host egg-shell rather than with a quantitative increase in intensity of movements of parasite larvae, etc. This is supported by the fact that hosts containing dead second or third instars of the larvae are rejected to an extent comparable with those hosts containing similar live larval instars' (p. 321). Lloyd's general conclusion, after a very interesting discussion of the whole question of instinct and perception, is that 'the oviposition response is to a perceptual complex of stimuli which is such that the female tends to choose these hosts in which its progeny are able to develop' (p. 321).

In the case of 'polyphagous' parasitic insects, which are not limited in their choice of a host for their eggs to one particular species or a small range of species, the perceptual clues which lead to the discovery of a suitable host are more

elusive and difficult to determine. A case of this kind has been elaborately studied by Thompson and Parker (1927). The polyphagous Chalcid *Melittobia acasta* parasitizes a wide range of larvae and pupae of Diptera and Hymenoptera, all characterized by being enclosed in a case or envelope, whether a cell or nest of mud or paper, a silken cocoon or a chitinized puparium. The general formula or definition of the host which appears to cover the observed cases is given as follows:—

‘(1) It must be at least twice the size of the parasite and usually much larger than it.

‘(2) It must be surrounded by an envelope of some sort which may be hard or soft, provided that there is a space between the body of the host and the envelope. Hosts with a hard cuticula firmly attached to the hypodermis are in general unacceptable.

‘(3) In nature, the most favoured hosts appear to be thin-skinned larvae or pupae surrounded by a protective envelope of some sort, the eggs being deposited upon the body of the victim, either through this envelope or directly upon it, after the parasite has made its way into the interior of the envelope’ (pp. 15–16).

Although, as Thompson and Parker point out, this characterization of the kind of host selected is a very general one, it seems possible that *Melittobia* makes its choice on the basis of size and the existence of an envelope separate from the larva or pupa within. It may be noted that *Mormoniella vitripennis*, which oviposits in the pupa of *Calliphora* (which it finds by smell), will not lay its eggs unless the ovipositor encounters an air space between the pupa and the puparium (Jacobi, 1939, quoted by Crombie, 1941).

More puzzling is the case of the Tachinid *Compsilura concinnata*, which parasitizes a very wide range of Lepidopterous and Tenthredine caterpillars—some fifty different species in Europe and over ninety in North America. The caterpillars it attacks are very diverse in appearance; they are of all colours, smooth or hairy, armed or unarmed, with or without poisonous hairs; they have different habits and habitats, and feed on all sorts of plants, so that they have, presumably, very diverse scents. It is true they are all caterpillars, but this definition includes a vast number of hosts which *Melittobia* does not attack. The problem as to what valent characteristics distinguish the selected caterpillars from the rejected is so far quite unsolved.

Summing up this discussion of instinct and perception, we may provisionally conclude that each animal species has an innate predisposition to perceive, and act with reference to, particular objects and events, which alone have valence for

it. It appears also that these objects and events are, in normal circumstances, biologically significant in relation to its special mode of living, of satisfying its needs and requirements and of perpetuating its kind. We have clear indications too that in many cases the biologically suitable object, such as, for example, the right kind of host in which to oviposit, is distinguished in perception from others less suitable by means of a few valent characteristics, such as a specific smell, size or shape, often linked with one another. These are, for the animal, perceptual or sensory clues or signs, to which it is predisposed or pre-adapted to attend, and they normally indicate, sufficiently well, the biologically suitable object. These signs are, therefore, *normally adequate*.

The possibilities of perception are, of course, limited by the animal's sensory equipment. What an animal *can* see depends upon the nature of its visual receptors; one does not expect fine visual perception from a frog or a mouse, or vision at all from an earthworm. The general character and scope of an animal's sensory and perceptual field is clearly determined by its sense organs; an orb-spider lives in a sensory world in which tactile and vibratory impressions are all-important, a bee in a world of specific scents, colours and shapes.

But the point of interest is not so much the sensory limitation and specialization of the possible perceptual field, but the fact that not all the potentially perceptible objects and events in the sensory field are valent, but only, as a rule, those that are biologically significant. Thus the honey-bee is specialized to attend instinctively to the scents of flowers, and cannot be trained to other scents, although its olfactory sense is highly developed; also it pays particular attention to images or figures that resemble or suggest flowers, and much less to images of unbroken contour (refs. in K. von Frisch, 1937)—it has an instinctive predisposition to seek out flower-shapes.

To many objects and events in its physical environment the animal remains behaviourally neutral; it does not notice them; they possess no valence for it. Only a few events will rouse it to attention and action. Here is an example. The slow-worm *Anguis fragilis* is, according to Wood Jones and Porteus (1929), singularly irresponsive to what goes on around it, 'but let anyone who wishes to test its powers of vision . . . arrange that a little grey slug shall wander into the picture and note the instantaneous effect that this produces on the Blind Worm. The little grey slug is a biologically relevant stimulus, since in the ordinary way *Limax agrestis* forms the elected article of diet of *Anguis fragilis*.' Now what the blind worm perceives is not 'a slug', as we perceive and recognize it, but merely something of a particular size, shape and mode of motion, which has food-valence. We must

carefully guard against the fallacy of assuming that animals perceive objects in the detailed and complex way that we do, as continuing 'things', recognizable by a large number of associated characteristics (see Russell, 1938, Chapt. x); the evidence tends to show, on the contrary, that animals may attend to and perceive only one or few characters of objects. That is why their perception sometimes leads them astray.

Many of the so-called aberrations of instinctive behaviour are quite understandable when we realize these two things—(1) that the animal's sensory or perceptual field is often a very simple one, and (2) that *in normal conditions* the events and the objects possessing valence are *usually* objects and events that are biologically significant. 'Aberrations' occur when, in unusual circumstances or by exception, the valent characteristic or clue crops up as a character of a biologically unsuitable object. But the animal does not necessarily confuse the two different perceptual objects—the suitable and the unsuitable; it may perceive only the valent characteristic which is common to both, and fail to perceive the differentia of the two. Within the limits of its instinctive perception, then, it does not err or make a mistake; it is misled.

The fact that the sensory or perceptual field is usually a fairly simple one helps in some measure to reduce the mystery of instinctive behaviour; we have no need to assume that an animal is attuned by heredity to recognize, without prior experience, a highly complex and specific object, such as it appears to us; it may be guided by some quite simple characteristic of the object, which alone is valent or perceived—the heat radiated from it, its smell, or its mode of motion.

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